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JOURNAL OF ANATOMY

THE SUBLINGUA AND THE PLICA FIMBRIATA.

By FREDERIC WOOD JONES, *Professor of Anatomy in the University, London, School of Medicine for Women.*

THAT the curious structure known as the sublingua in the Lemurs should be the expression of any very primitive condition is an assumption which, though commonly made by comparative anatomists, is not likely to impress anyone who is familiar with the habits of Lemurs as being at all probable.

If one were asked to point to a peculiarly highly-specialised structure, one that had been definitely elaborated in response to a functional need, it would be difficult to select a feature more satisfying than the lemurine sublingua. This curious structure is one that cannot rightly be understood by studying it merely as a fold upon the under surface of the tongue; it must be correlated with other details of the anatomy of the mouth and must be observed in the living animal. The incisor teeth of the typical Lemurs are peculiar; the lower ones being strikingly elongated and set at such an angle in the jaw that their "biting" edges face directly forwards instead of being directed upwards towards the upper incisors.

Moreover, it is evident that these peculiar lower incisors have some function which is not shared by the upper incisors, for the incisor series of the upper jaw is composed of somewhat rudimentary peg-shaped teeth which are evidently not exercising their full functional rôle. They are not engaging the lower incisors in any action of biting, and in adult skulls they are very commonly in an extremely reduced condition. More than this, the lower incisors are reinforced by the lower canines which, assuming the same elongated form, become procumbent with the incisors, and are at times mistaken for members of the incisor series.

Following upon this change in the lower canines, the first lower premolars have assumed the rôle and form, but not the position, of true canines, and have added to the confusion produced in the minds of some who have dealt with this question (see fig. 1). This curious arrangement of the lower incisors and canines is a very striking one, and there can be no question as to its purpose, since these teeth play little or no part in the

process of alimentation, but are specialised purely as a hair comb. So far as I know, this function was first detected by Cuvier, who, writing of *Lemur catta*, said that the lower incisor teeth "sont de véritables peignes" (*Hist. Nat. Mammif.*, 1829, p. 218). Hair combs and feather preeners have been evolved *de novo* time and again, and from a series of very different structures. There is no need to turn aside to the curious serrated claws of such birds as *Fregeta* or *Sula*; for a hair comb, which is also derived from the front teeth, is present so much nearer to hand in *Galeopithecus*. The dental hair combs of the true Lemurs and the so-called Flying Lemurs afford striking examples of parallel evolutions in response to functional demands, for though the end attained is the same

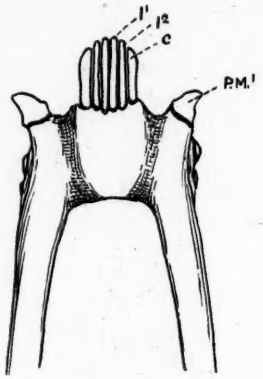

FIG. 1.—Anterior teeth of the lower jaw of *Lemur catta*, seen from below.

in the two cases, the method of making the comb is strangely different. In *Lemur* the incisors and the canines are ranged parallel and procumbent like the "teeth" of a comb; in *Galeopithecus* the biting edges of the individual incisor teeth have become finely serrated, and each tooth therefore furnishes many "teeth" for the comb; this method may be said to constitute an economy of incisors as hair combs, and the canines therefore do not join the incisor series, but on the other hand become modified in the direction of the molar series.

These two animal types have developed these dental hair combs probably for the reason that special adaptations have rendered it difficult to perform the toilet of the woolly hair by scratching—the Lemurs having no free claws upon the fingers and only one specialised one on the toes, and the limb of *Galeopithecus* being hampered by the flying membrane. In the case of the

Lemur the application of the hair comb is an oft-repeated business, and one that is very easy to observe in all its details.

With the development of this very highly-specialised dental structure there has arisen a need for specialised toothbrushes, and again it is of interest to note that the two forms have evolved entirely different forms of organs for this purpose. In *Galeopithecus* the anterior edge of the tongue is finely serrated in harmony with the serrated incisors, a very efficient toothbrush being provided for the hair comb. *Lemur*, on the other hand, has developed some structure beneath its tongue into a horny leaf-like organ which is finely serrated along its edges and sharp-pointed at its tip (see fig. 2). The use of this structure as a toothbrush has, I believe, been

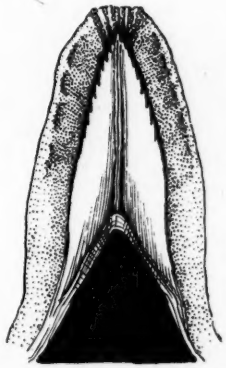

FIG 2.—Tongue of *Lemur catta*, seen from below, to show the plica mediana and plicæ fimbriatæ.

long familiar to Mr R. I. Pocock, and there can be no doubt whatever that the "sublingua" of *Lemur* is a purely functional organ, evolved from some part of the tongue for the purpose of cleaning the functionally specialised lower incisor teeth.

Such facts as these show the lemurine sublingua in rather a different light from that by which it is regarded as an inherited and functionless rudiment of some premammalian ancestral structure. But even though it is in *Lemur* a functional, highly-developed, and specialised structure, it is of necessity made from some basis which other mammals must possess in some degree. This basis is a curious one, and one that is so variable in its manifestations that its most primitive expression in the mammals must remain somewhat uncertain.

Nevertheless, one particular basal type appears to embrace all the

modifications so far met with, and that will be described provisionally as the ideal form.

This form finds expression in certain Marsupials, a few Eutherian adults, and several Eutherian embryos.

In this type, the tongue bears no papillæ whatever upon its under surface. There may or may not be a median strengthening elevation extending from base to tip; but upon either side of the middle line, starting near the middle line at the free tip and diverging as they proceed backwards, are folds with projecting edges which are covered by thickened horny epithelium. The free edges of these folds may be variously serrated. At the attached base of the tongue they turn forwards and downwards towards the floor of the mouth as two crenated folds that terminate

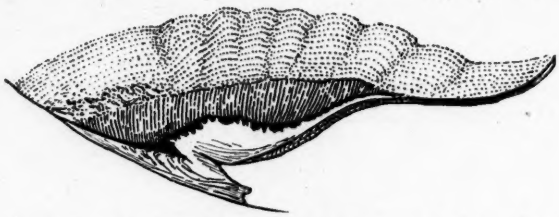

Fig. 3.—Tongue of *Petaurus breviceps*. The continuity of the plica fimbriata with the plica sublingualis is well seen.

near the middle line of the floor of the mouth not far behind the symphysis menti.

At the point where the fold upon the side of the tongue curves forwards to join the fold on the floor of the mouth a common fold runs backwards along the attached margin of the tongue and here becomes gradually lost (see fig. 3). In many cases it would probably be more correct to describe this last fold as running along the side of the posterior portion of the tongue and floor of the mouth, subsequently bifurcating into one fold which runs along the side of the tongue, and another which runs along the floor of the mouth. Any or all of these folds may be finely serrated, more coarsely dentated, merely crenated, or practically plain. Since the lemurine toothbrush is an elaboration of the fold upon the free portion of the tongue, it is natural to inquire if the whole basal structure may not have some such function, and that this is the true explanation of the presence of these folds appears to be extremely probable. Such a view is strengthened by the fact that their development is certainly not an isolated thing, for upon the outer side of the dental series an exactly similar serrated fold is, in many animals, produced from the lower lips

and cheek folds. This curious fold is well seen in the dog, and, so far as I know, no purpose has ever been ascribed to it; but I believe its true rôle is a cleanser of the teeth, and that the same service is performed within the mouth by the folds which lie below the tongue. It must be remembered that, although in Homo the tongue may explore and cleanse the whole dental series, the relation of the tongue, teeth, and floor of the mouth forbids a lingual exploration of the molar series in many animals. In the new-born Palæarctic wolf figured (fig. 4) the condition is very remarkable, for here the labial folds outside the dental series are associated with serrations of the side of the tongue within the dental series. This is another lingual toothbrush, which, as in *Galeopithecus*, is not formed from

FIG. 4.—New-born cub of Palæarctic wolf with cheek removed, to show the lip fold and the dentated side of the tongue.

a fold beneath the tongue but by the papillated surface of the tongue itself. Although I gather from Professor Wright that the use of the tongue as an organ for cleansing the teeth had impressed Leonardo da Vinci and had prompted him to some speculations upon this very point, it must be confessed that this aspect of the tongue as a functional structure has subsequently become rather overlooked.

In order to follow the fate of the specialised folds which lie below the tongue it is necessary to adhere to a precise nomenclature, and reference will be made again to a tongue such as that of *Petaurus breviceps*, which appears to show all the folds in fairly full development (see fig. 3).

The median strengthening rod is known as the *plica mediana*, and it is an expression of a sublingual development of the septum of the tongue. It is an extremely variable structure. The midline of the under surface of the tongue may be elevated, flattened, or depressed, for the

thickening of the septum as a supporting structure may take place within the substance of the tongue or below its inferior surface. In *Petaurus* it is a well-marked free ridge upon the under surface of the tongue. It is this structure which finds one form of expression in the "lyssa" or

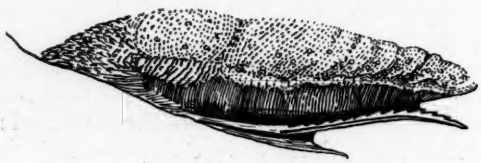

FIG. 5.—Tongue of *Lemur catta*. The plica fimbriata forms the well-developed sublingua. The plica sublingualis has practically ceased to exist.

"tollwurm" of the dog's tongue. In *Lemur* it constitutes the median ridge of the "sublingua."

The fold which runs from the tip of the tongue towards its attached base is the *plica fimbriata*, and the fold which runs from the posterior portion of the tongue to the floor of the mouth beneath the tongue is

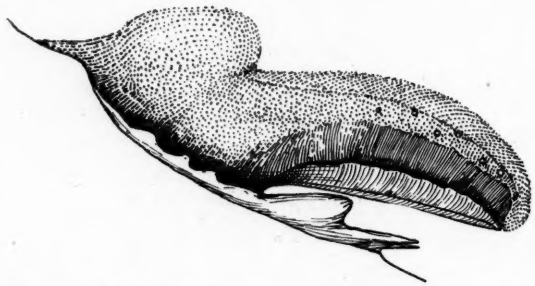

FIG. 6.—Tongue of *Tarsius spectrum*. Plica mediana, plica fimbriata and plica sublingualis are all well developed.

the *plica sublingualis*. This fold at its anterior limit in the floor of the mouth marks the site of the openings of the submaxillary salivary gland, and may be reduced to a structure no more prominent than the so-called Wharton's papilla or caruncula.

The present paper is concerned simply with the comparative development of these folds within the limits of the order Primates, as that order is at present constituted.

In the Lemurs the characteristic features are determined by a great

development of the plicæ fimbriatæ, which constitute a highly-specialised organ adherent to the tongue over the great extent of its length and supported in the middle line by the plica mediana. This structure composes the "sublingua" of the Lemurs. The tip of the sublingua is

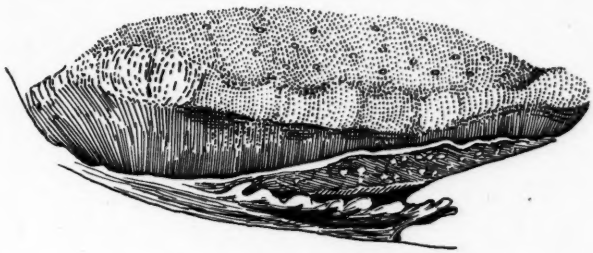

FIG. 7.—Tongue of an adult Chimpanzee. Plica fimbriata and plica sublingualis both well developed.

free of the under surface of the tongue for a short distance. In all the Lemurs the plica sublingualis is an extremely rudimentary structure, entirely wanting upon the side of the tongue, and represented merely by minute carunculæ on the floor of the mouth.

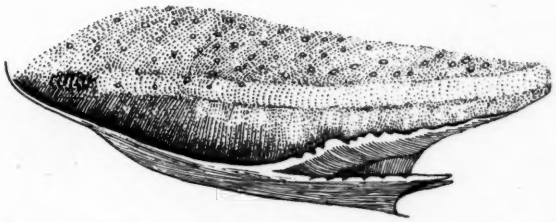

FIG. 8.—Tongue of a human fœtus. Plica fimbriata and plica sublingualis are both well developed.

The development of the plica mediana and a conspicuous "sublingua" derived from the plicæ fimbriatæ upon a somewhat lemurine model is seen in the Didelphia in *Trichosurus vulpecula*, but in this type the plica fimbriata is by no means so highly specialised as it is in Lemur.

The tongue of *Tarsius* stands in very marked contrast to anything seen in the Lemurs, for here all those parts which we have pictured as being components of the generalised condition are fully developed (see fig. 6). The plica mediana is strongly marked. The plicæ fimbriatæ occupy a relatively large area of the under side of the tongue, and they

are adherent to it in the whole of their length. The plica sublingualis is conspicuous, and shows a well-marked crenated edge. Histologically these folds show a well-marked thickening of the surface corneous layers such as is present in the almost horny "sublingua" of the Lemurs.

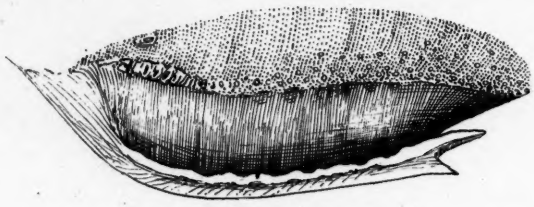

FIG. 9.—Tongue of *Macacus nemestrinus*. The plica sublingualis is well developed. The plica fimbriata has disappeared.

In the study of the interrelations of the different members of the order Primates the tongue of *Tarsius* is of the utmost importance, since no other members of the order save Man and the Anthropoids show this

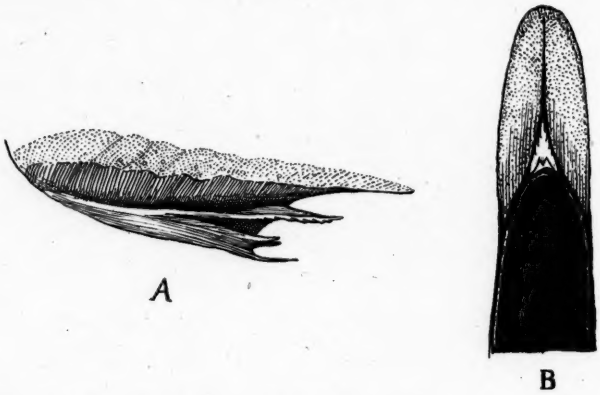

FIG. 10.—Tongue of a Marmoset (*Callithrix penicillata*). A, from the side; B, from below. The plica fimbriata is well developed; the plica sublingualis, though small, is large for a New-World monkey.

generalised condition of these folds. In the first place, it must be noted that the tongue of *Tarsius* differs entirely from that of any of the Lemurs in the possession of the plicæ sublinguales in a condition of full development, that it is of the generalised form, not widely different from that of *Petaurus*, a condition from which presumably the Lemurs have specialised

just as *Trichosurus* has departed in a somewhat lesser degree. In the train of *Tarsius* the tongues of the Chimpanzee (fig. 7) and of Homo (fig. 8) follow very closely, for in both types the two folds are well developed. But among the Primates they stand alone in this generalised condition, for all the monkeys of the Old World and the New are specialised in one direction or the other from this generalised form. In

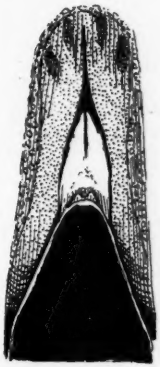

FIG. 11.—Tongue of *Cebus albifrons* from below, showing well-developed plicæ fimbriatæ and minute plicæ sublinguales.

the Old-World monkeys the plica fimbriata is absent and the side of the tongue is entirely smooth, but the plica sublingualis is fairly well developed (see fig. 9). In the New-World monkeys the plica fimbriata is usually well developed and the plica sublingualis though present is not conspicuous (see fig. 11). In the Marmosets it attains a fair degree of development, but in other genera it is reduced to the merest rudiment (see fig. 10).

In none of the New-World monkeys, however, is the plica fimbriata developed into such a highly-specialised structure as the "sublingua" of the true Lemurs.

A HITHERTO UNDESCRIBED MALFORMATION OF THE HEART.

By H. Blakeway, M.S., F.R.C.S., *Surgical Registrar, formerly Demonstrator of Anatomy, St Bartholomew's Hospital.*

(From the Anatomy Department, St Bartholomew's Hospital.)

The specimen described below was sent to me in 1912 by my friend Dr J. A. Bell, M.C., Captain R.A.M.C. (T.), who was at that time Medical Officer at Camberwell Workhouse; I am greatly indebted to him for giving me the opportunity of examining and describing it.

The heart (which is now in the Museum of the Royal College of Surgeons of England) is that of a male infant, born in the workhouse; the child, which weighed 7 lbs., survived only thirty-eight hours. Other clinical details are lacking.

Unfortunately the specimen suffered considerably in the process of removal from the body—the more unfortunately, because it shows a condition which, so far as I am aware, has not up to the present been described, namely, that the aorta, though of normal size, has no communication with either ventricle, but was filled from near the apex of the left ventricle by way of the anterior interventricular branch of the left coronary artery.

In fig. 1 the heart has been drawn so as to show most of its abnormalities. There is a very obvious disparity in the size of the cavities of the right and left sides of the heart: this affects especially the auricles, the right auricle being large, while the left is remarkably smaller than normal.

The *right auricle* shows the normal division of its interior into two parts by a prominent crista terminalis, behind which is a large opening of the inferior vena cava; that of the superior vena cava appears to have been, in part at least, cut away; no Eustachian valve is present. At its left lower extremity the right auricle receives the wide opening (unguarded by any valve) of the left horn of the sinus venosus, which becomes continuous, round the left side of the left auricle, with a persistent left superior vena cava; a great cardiac vein is present in the left auriculo-ventricular furrow, and also opens into the sinus.

Enough of the interauricular septum remains to show that the foramen ovale was widely open.

The right auriculo-ventricular orifice and the tricuspid valve (fig. 2) show no gross abnormalities, though the cusps of the valve are unusually large. The opening measures 15 mm. in its longest diameter.

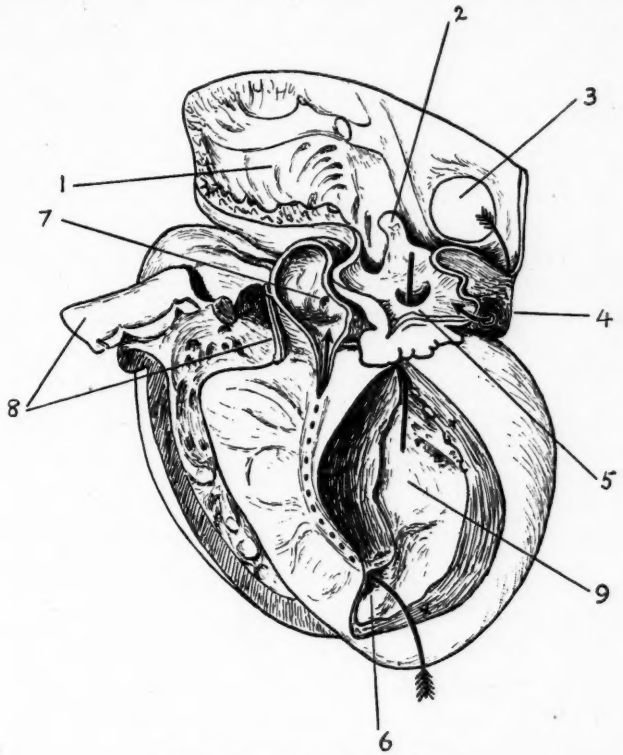

FIG. 1.—General view of the specimen.

1, right auricle; 2, interauricular septum, with patent foramen ovale; 3, opening of inferior vena cava; 4, left horn of sinus venosus and left superior vena cava, from which arrow emerges; 5, cavity of left auricle; a rod passes through the mitral orifice; 6, the abnormal communication between the left ventricle and the anterior interventricular coronary artery; a bent arrow passes along the latter into the aorta; 7, the point of origin of the right coronary artery from the aorta; 8, commencement of the pulmonary artery, in two pieces; 9, left side of interventricular septum; above is seen the oblique ridge which divides the cavity of the left ventricle into two parts.

The *right ventricle* shows considerable enlargement, which is confined to the body of the ventricle, the infundibulum, although it does not appear to be smaller than normal, being disproportionately small as compared with the rest. The cavity is seen to extend behind the left ventricle as far as

the left margin of the heart, the septum between the right and left cavities being very obliquely placed.

Only the very commencement of the pulmonary artery is preserved, and that in pieces, but it is clear that the orifice was approximately of normal size; and it has a normal valve with three cusps.

The *left auricle* (fig. 1) is many times smaller than the right; no pulmonary veins are seen opening into it; and although they may have

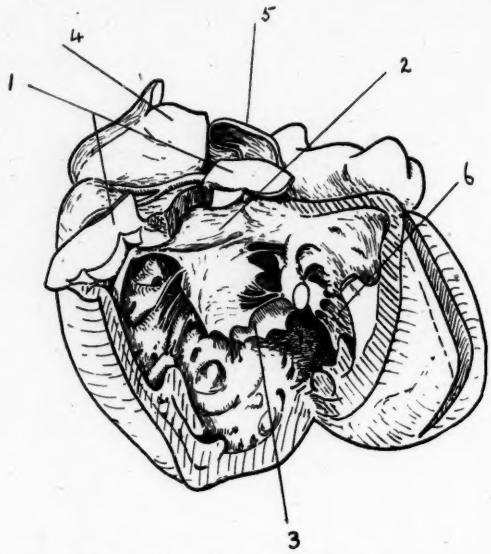

FIG. 2.—The right ventricle has been widely opened.

1, the two parts of the pulmonary artery; 2, infundibulum of ventricle; 3, tricuspid valve; 4, right auricle; 5, ascending aorta; 6, right side of interventricular septum; the septal cusp of the tricuspid valve is applied to its upper part. Note the cavity of the ventricle, in shadow, carried far to the left behind it.

been cut away, yet the incised wall of the auricle can be brought together in such a way as so nearly to reconstruct the chamber that it is difficult to see how the veins could have reached it. There is a small auricular appendix, with miniature musculi pectinati in its interior.

From the auricle a smooth, rounded mitral orifice, 4 mm. in diameter, leads into the *left ventricle*; this latter is of approximately the normal size, and has a well-developed muscular wall; but in almost all other respects it is a highly abnormal chamber. Its upper sixth part is partially separated from the rest by a prominent oblique muscular ridge (see figs. 1 and 3).

The two parts are very different in appearance and connexions; columnæ carneæ, though small, are prominent features of the ridge and of the upper subdivision of the cavity: certain of them are developed into musculi papillares, which have attached to them the chordæ tendineæ belonging to the two tiny cusps of the mitral valve. But in the lower subdivision muscular columns are absent: the endocardium is smooth, becoming thicker and opaque towards the apex, where also it is somewhat puckered.

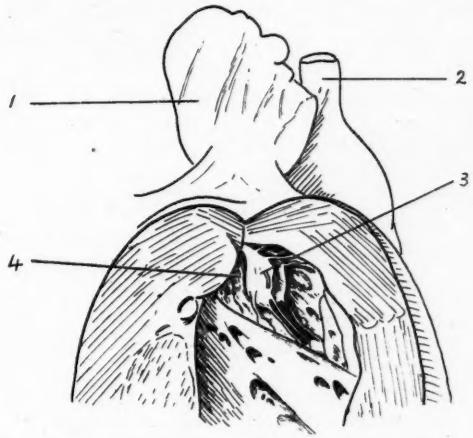

FIG. 3.—Enlarged view of part of the left ventricle, opened widely to show the upper subdivision of the cavity, bounded below by a thick muscular ridge.

1, left auricle, turned up; 2, left superior vena cava; 3, anterior cusp of mitral valve; 4, the blind angle between the anterior cusp of the mitral valve and the uppermost part of the interventricular septum.

The interventricular septum is entire, and of good thickness throughout its extent; the part of it that is related to the upper subdivision of the left ventricle has applied to its right side the septal cusp of the tricuspid valve; on the left side (see fig. 3), where it should lead up to the aortic orifice, no such opening is to be seen, the narrow space between the septum and the anterior cusp of the mitral valve ending in a blind angle above.

The question as to how the ventricle emptied itself is solved by an examination of its lower portion; here, near the apex, the cavity bends forward and to the right, and narrows to a funnel-shaped opening, 2 mm. in diameter, which leads directly into an anterior interventricular channel on the surface of the heart: at the junction of this vessel with the cavity

of the ventricle the channel is slightly narrowed by an irregularly circular thickening of the endocardium (fig. 4).

This remarkable vessel is the only communication between the left ventricle and the aorta; it passes upwards, accompanied by a microscopic cardiac vein, in the anterior interventricular groove, displaying in its interior the origins of several branches which pass obliquely upwards and laterally to the walls of the ventricles: it then opens in a funnel-shaped fashion into the commencement of a well-developed ascending aorta.

This interventricular vessel is, beyond doubt, the anterior inter-

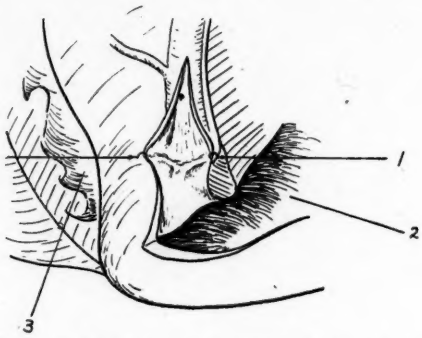

FIG. 4.—Enlarged view of the communication between the apex of the left ventricle and the anterior interventricular coronary artery.

The point of communication is hooked open (at 1) to show the slight transverse constriction; 2, cavity of left ventricle; 3, cavity of right ventricle.

ventricular branch of the left coronary artery; this, not only from its position and connexion with the aorta, its supply of vessels to the heart wall, or its microscopic structure (see fig. 6), but still more from the fact that the main trunk of the left coronary is seen arising from within the funnel-shaped upper end of the vessel, and then running to the left in the auriculo-ventricular furrow (fig. 5).

Examination of the beginning of the ascending aorta places the identity of the coronary vessel further beyond question. The aorta, as has been said, does not communicate with the base of the left ventricle; but its interior, in the situation where the communication should be, shows a shallow depression, divided into two lateral parts by a very low ridge: from the right-hand portion arises a normal right coronary artery. It is impossible to doubt that these shallow depressions represent two of the sinuses of Valsalva; and a less distinct indication of the third is seen where

the left coronary artery communicates with the aorta. The relation of these shallow depressions to one another and to the pulmonary artery will be recognised as being normal.

When this specimen was demonstrated to the Anatomical Society information as to certain points which have since been made clear by further dissection was lacking, and considerable doubt was expressed as to the correctness of the interpretation of the specimen given above. It

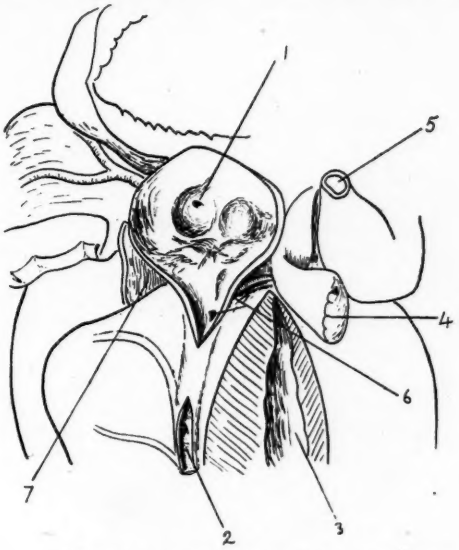

FIG. 5.—Enlarged view of the interior of the commencement of the aorta.

1, origin of right coronary artery from one of the rudimentary sinuses of Valsalva; 2, anterior ventricular branch of left coronary artery; within it is seen the opening of one of its branches to the right ventricle; 3, cavity of left ventricle; 4, left auricular appendix, turned aside; 5, left superior vena cava; 6, main trunk of left coronary artery; 7, part of pulmonary artery.

was suggested that the vessel seen in the anterior interventricular groove might not be a coronary artery, but that it might rather represent a part of the bulbus cordis, the aperture near the apex of the left ventricle being the ostium bulbi. Such a suggestion was at the time a tempting one; it gave prospect of a reasonable explanation, based on embryological knowledge, for an otherwise inexplicable condition. Indeed, the striking difference between the two portions of the left ventricle suggested that possibly only the small upper subdivision was really the ventricle proper,

the ostium bulbi being at the level of the muscular ridge marking the communication between the two portions of the cavity (figs. 1 and 3).

Microscopic examination of the ventricular wall from each portion of the chamber does not lend support to this view. Sections were made at the two points marked with crosses on the cut surface of the ventricle in fig. 1; they show no essential difference in structure: near the apex the muscle is much thinner, and, as the naked-eye examination suggests, the endocardium is thick (fig. 7), and beneath it bundles of cellular fibrous

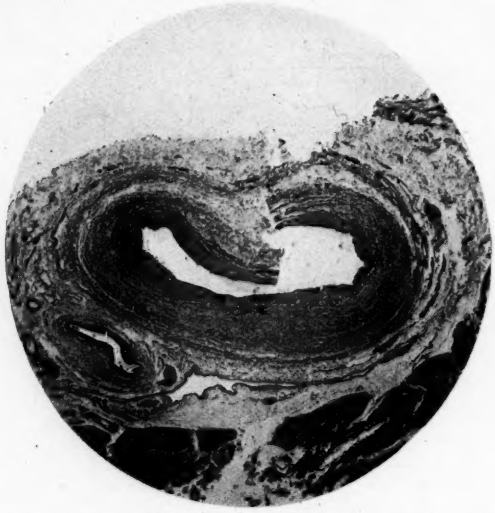

Fig. 6.—Transverse section through middle of anterior interventricular coronary artery and accompanying cardiac vein. × 19.

tissue, with a structure similar to that of the surface endocardium, pass in places between the muscular fasciculi—an appearance which is not seen in the upper section of the ventricle.

But the section of the wall of the left ventricle near its apex is very different from that of the interventricular channel conveying blood to the aorta; the microscope confirms the conviction formed by dissection that this vessel is an artery, the interventricular branch of the left coronary (see fig. 6).

While the connexion of this artery with the left ventricle and the total obliteration of the normal aortic orifice seem at present impossible of satisfactory explanation, certain conjectures may be hazarded.

The two conditions are no doubt interdependent. The aorta did originally arise widely and directly from the ventricle; all that we know of its development, the saccular depression at its commencement, and the rudimentary sinuses of Valsalva, all make this certain. The obliteration, then, was a late process, occurring after the truncus arteriosus had been separated into its pulmonary and systemic parts. Was it the result of the abnormal communication between the coronary artery and the ventricle, or was the aortic orifice first obliterated, and the coronary communication opened up

FIG. 7.—Section through wall of left ventricle in the position of the lower of the two crosses seen on the cut surface of the ventricle in fig. 1. × 35.

as a result? If the obliteration of the aortic orifice was the primary condition, we may suppose a pathological inflammatory process to have been probably at work; but perhaps not necessarily so: in the young embryo, the facility with which parts fuse together which before were distinct is only matched by the ease with which solid tissues may become pervious. But our wonder is constantly excited, not only by the rarity with which complex developmental processes go awry, but nearly as much by the fact that when they do so the very malformations are generally subject to laws, and are readily recognised, though not explained, as arrests of development and their results.

No arrest of development will explain the obliteration of the aortic

orifice seen in this heart, for from the earliest stage of its development the aorta and the ventricle are in free communication. The stenosis is an *irregular* abnormality; but since the causes, whatever they may be, which lead to abnormal development do not act entirely capriciously, it would be unreasonable to suppose that this irregular aortic stenosis was in fact capricious. The possibility of the process being syphilitic has to be considered. The mother cannot be traced; but the sections of the coronary artery and of the heart wall do not suggest a syphilitic lesion, and such an explanation would fail to cover the other anomalies seen in the specimen.

Less unlikely, then, than an explanation depending on a merely capricious (because causeless) closure, or upon an inflammatory stenosis of the aorta, is the view that the aperture into the coronary artery from near the apex of the ventricle may have been the primary anomaly, the aortic closure resulting from this.

While no details as to the development of the coronary arteries are yet known, it seems not impossible that during the absorption of the muscular sponge-work in the formation of the ventricular cavities such an abnormal communication between ventricle and coronary arteries might arise: the sharp difference between the upper and lower subdivisions of the ventricular chamber appears susceptible of some similar explanation, *i.e.* that the smaller upper subdivision alone is the ventricle proper, matching the auricle in size, while the lower part is an abnormal cavity formed by the opening up of the muscular sponge-work belonging rather to the right ventricle than the left. The meaning of the obliquity of what has been called above the interventricular septum, and of the extent of the right ventricle behind it to the left border of the heart, would thus become apparent. If then, as in this heart, extreme under-development of the left auricle and ventricle already existed, and the blood-flow through the left side of the heart were consequently much diminished, even such an apparently small cause as the opening up of the ventricle into the coronary artery might produce so great a result as the closure of the orifice of the aorta.

SOME INDICES AND MEASUREMENTS OF THE MODERN FEMUR.

By J. R. D. Holtby, M.D., Sc.B., *Chief Demonstrator of Anatomy, Trinity College, Dublin.*

This investigation was originally undertaken in order to ascertain the average degree of pilastring in modern femora, but gradually the work was extended to include other points of interest.

The specimens here dealt with were taken from the bones ordinarily in use for teaching purposes in the Anatomical Department of Trinity College, Dublin. Bones with obvious irregularities due to disease were rejected, but with this exception no attempt was made at selection, the object being to obtain as representative a series of average conditions as possible. It is to be regretted that no opportunity has so far offered itself of obtaining femora definitely known to be in pairs, and herein lies, perhaps, the greatest objection to some of the conclusions which have been arrived at. An endeavour is now being made to get together a series in which great care has been taken to make the pairing and sexing absolutely definite and known.

The measurements were all made and the various indices calculated before it was attempted to subdivide the collection into groups according to sex and side. This resulted in some irregularity in the numbers in the various sections, but is not a serious disadvantage. The bones were sexed by Parsons' method, and as all the measurements, etc., are given in the various portions of Table I., it is comparatively easy to see how many possible mistakes have arisen. Only a small proportion presented any great difficulty as regards sexing, and these were carefully considered several times before being finally allocated to their special group. The measurements were all checked, in some cases several times, and may be taken as accurate.

Parsons advocates consideration of the following points in endeavouring to ascertain the sex of a femur:—

1. Diameter of head—estimated with callipers held parallel to long axis of neck . . . – 44 ♀ + 48 ♂ mm.
2. Bicondylar width . . . . . – 70 ♀ + 75 ♂ „
3. Least transverse diameter of shaft . . – 25 ♀ + 29 ♂ „
4. Head length index . . . . . – 104 ♀ + 109 ♂
5. Platymeric index . . . . . – 75 ♀ + 90 ♂
6. Maximal length . . . . . – 40 ♀ + 45 ♂ cm.

The collection comprised 56 male bones, 35 from the left side and 21 from the right; of the remainder, 20 were of the right side and 24 of the left from female subjects.

Table I. in its four subdivisions gives the various measurements and indices of each of these groups, whilst Table II. shows the averages in each.

It will now be convenient to consider the various points in order.

Length.

Both oblique and maximum measurements were taken. The former is obtained by use of a measuring board, the two condyles lying flat on the foot plate, the caput against the upper plate.

The maximum length is the greatest length between the head of the femur and the under aspect of the medial condyle.

According to Pearson, the maximum length exceeds the oblique by 3·2 mm. in males and 3·3 mm. in females.

In my series, account was not taken of fractions of a millimetre in measuring the length, so I cannot refer to the decimal. In males it was sufficient to add 3 mm. to the average oblique length to get the average maximum on either side of the body; but among the female groups, whilst an addition of 3 mm. was required on the right side, 2 mm. was sufficient on the left. It must be remembered that the addition of these figures to the oblique measurement will only give the maximum length in the average; individual examples vary widely—in some cases as much as 6 mm. will have to be added, and in others the two measurements may be identical. Occasionally, indeed, the oblique length may even exceed the maximal.

There is no marked difference between the oblique and maximal lengths as regards sex, and a comparison of these measurements is thus of no utility as regards sex grouping.

Maximum length (average), cm.				Oblique length (average), cm.			
Male.		Female.		Male.		Female.	
Right.	Left.	Right.	Left.	Right.	Left.	Right.	Left.
45·3	46·0	41·4	41·6	45·0	45·7	41·1	41·4

It will be seen that there is a difference in the length of the bones from the two sides, which is more marked in males than in females. Of course

the bones in this collection were not in pairs, but Parsons, who noticed a similar condition in his Rothwell series, says that it is borne out by measurements of known modern pairs. In his series, however, the sexual element is not shown, the left bone in both sexes being 3 mm. longer than the right one. In my collection the left male bones were 7 mm. longer than the right ones, the left female specimens only 3 mm. longer than their fellows.

THE RANGE OF VARIATION IN OBLIQUE AND MAXIMAL LENGTHS.

	Maximum length.	Oblique length.
Males.		
Right	40·4–51·6 cm.	40·3–50·5 cm.
Left	41–52·3 ,,	41–52·1 ,,
Females.		
Right	37·4–45·2 ,,	37·3–44·6 ,,
Left	36·2–46·4 ,,	35·8–46·1 ,,

The curves on fig. 1 show the distribution of the variations in oblique length.

It will be seen that a bone with an oblique length of less than 40 is almost certainly female, whilst one with a measurement of over 46 is almost invariably male.

DIAMETER OF THE HEAD.

On reference to Table II. it will be seen that the average diameter of the head was almost the same on the two sides in female specimens, but that among males there was a considerable difference between the two sides. In Parsons' series the diameter of the head was not uniform in paired bones, but varied from 0·5 to 1 mm. The range of variation is shown as under:—

	Males.		Females.	
	Right.	Left.	Right.	Left.
Average . . .	48 mm.	49·6 mm.	42 mm.	41·5 mm.
Range . . .	43–51	44–56	37·5–45·5	37–46

The curves on fig. 2 show the distribution of the range. It may, of course, be objected that no deductions can be drawn from the figures in

this connection, as the diameter of the head was one of the factors relied upon for determining the sex to which a given specimen belonged. It will, however, be seen from the curves that it has not been allowed to act unless other points bore out its evidence, for there is a considerable amount of

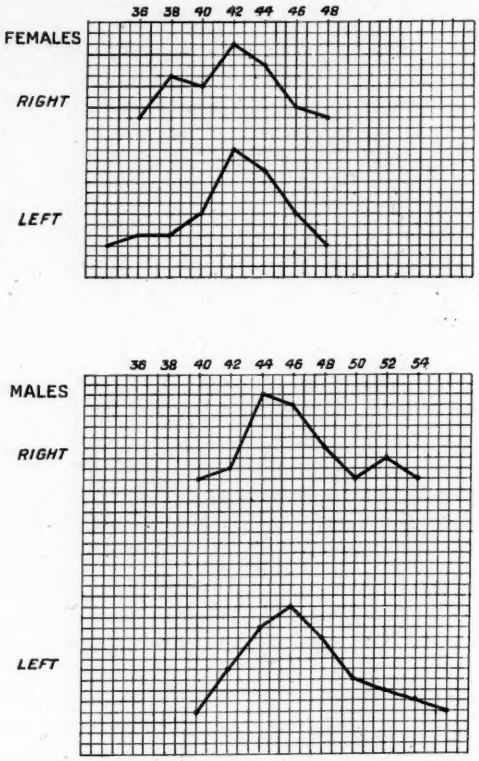

Fig. 1.—Curves to show variations in oblique length.

overlapping between the two sexes, especially between the 44 and 46 mm. limits. Bones under 44 were almost always females, and those over 46 were practically invariably males. It will be seen also that the height of the curve on both sides in female specimens corresponds to those with a diameter of 40 to 42 mm.; among male bones, the height of the curve is reached at 46 on the right side and at 48 on the left.

Relationship between Diameter of Head and Bicondylar Width.

The average relationship is shown below, the figures indicating that the bicondylar width was the given multiple of the diameter of head,

Males.		Females.	
Right.	Left.	Right.	Left.
1·6	1·5	1·6	1·6

so that the large diameter of the femoral head on the left side was not accompanied by a corresponding increase in the bicondylar width.

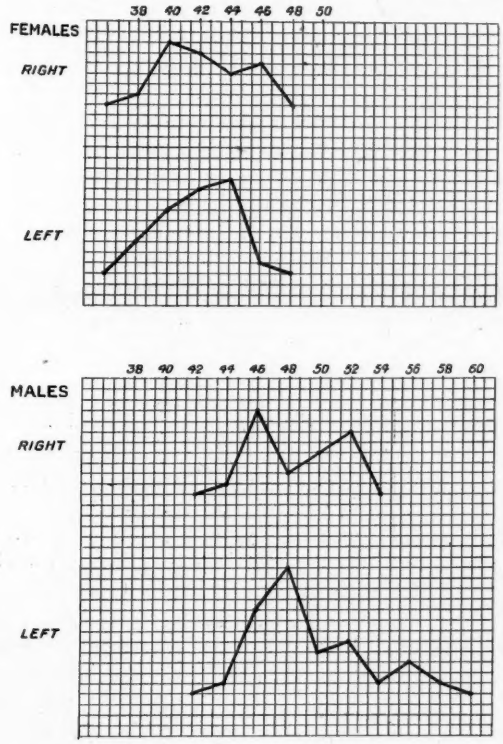

FIG. 2.—Curves to show the distribution of variations in the diameter of the femoral head.

The latter, as will be seen from Table II., is almost identical on the two sides.

Roughly, the average relationship for bones of both sides and sex is that the bicondylar width is 1·6 times the diameter of the head. The range of variation among individual cases is comparatively small (from 1·5 to 1·8), but is quite sufficient to allow of mistakes being made in estimating one measurement from the other; usually the error would not exceed 3 mm. in calculating the diameter of the head from the bicondylar width, but it may be as much as 8 mm. if the estimation of the bicondylar width be based on a known diameter of the head. Thus it might be difficult to accurately sex a bone with one damaged extremity unless the other indications were well defined. In Hepburn's series the bicondylar width was in the average 1·7 times the diameter of the head.

Head Length Index.

This was introduced by Parsons as a means of ascertaining the proportions of the diameter of the head to the length of the bone. If the head of the female be, as is stated, smaller than that of the male, not only absolutely but also relatively to the length of the femur, the index should show sexual differences. The maximal length of the bone is divided into the diameter of the head multiplied by 1000, and an index is thus obtained. The multiplication by the figures 1000 is only done in order to show the result as a whole number to allow of ready comparison.

	Males.		Females.	
	Right.	Left.	Right.	Left.
Averages . . .	105·5	106·4	102·5	100·2
Range . . .	96·6-118·2	96·3-121·7	93·6-107·4	87-108·7

Thus there appears to be on both sides too much overlapping, as Parsons pointed out, to render the index useful for sexing except at the extremes; bones with indices of over 108 are usually males, whilst those with indices below 96 are almost invariably females. Generally speaking, the head length index is smaller in long bones than in short ones, the latter having relatively large heads. See curves on fig. 3 (*a*).

Bicondylar Width.

Parsons recommends that this be measured with a sliding scale, the condyles lying flat on the long stem, the limbs of the scale touching

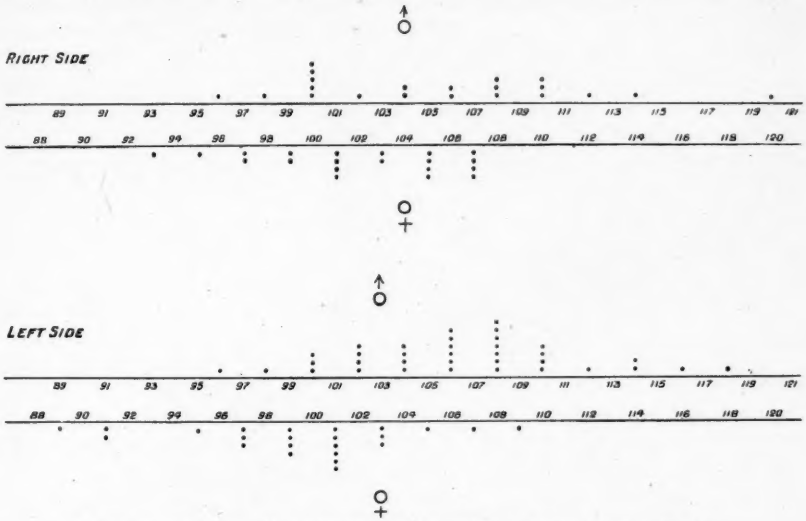

FIG. 3.—Chart to show the distribution of the variations in the head length index.

the condyles close to their articular margins. As can be seen from Table II., the measurement on the average is practically the same on

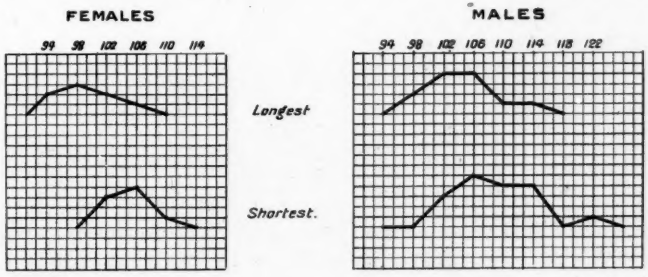

FIG. 3 (*a*).—Curves to show head length indices in longest and shortest bones.

either side. There is an important sexual difference corresponding to that of the diameter of the head, as is well seen in the curves on fig. 4.

The maximum point for female bones was at 70, irrespective of side; among the male specimens, however, the maximum distribution point is reached at 76 on the right side, whilst on the left it is between 76 and 80. Bones with a bicondylar width of under 72 are, almost certainly, female, those with a measurement of over 74 being usually male (Parsons stated

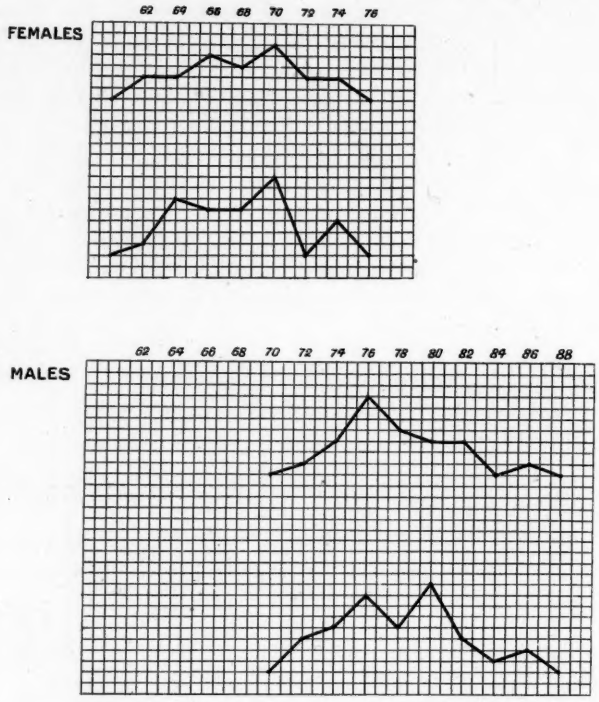

FIG. 4.—Curves to show variations in bicondylar width. The upper curves represent specimens from the right sides, the lower from the left.

that between 70 and 75 the sexual factor was indefinite). It will be noted that left-sided bones more especially seem to show specimens in or near the sex limit points.

Relationship of Bicondylar Width to Oblique Length.

Although averse to the multiplication of indices, I have found it convenient to use one to show this relationship. It is based on the one

introduced by Parsons as the head length index, and is obtained by dividing the oblique length in millimetres into the bicondylar width multiplied by 1000. If one selects the longest and shortest bones from any series, it will be seen that there is, in the great majority of cases, a striking variation in the index, short bones having relatively broad lower extremities. The following averages show this:—

Males.		Females.	
Longest bones (12). .	Average index 163	Longest bones (8). .	Average index 158
Shortest ,, (17). .	,, ,, 174	Shortest ,, (9). .	,, ,, 169
Average ,, (12). .	,, ,, 171	Average ,, (12). .	,, ,, 165

The figures as to the index in bones of average length are given to complete the comparison, but among them the range of variation is very great. The curves on fig. 5 show the variation for the longest and shortest specimens, and indicate that although there is a considerable

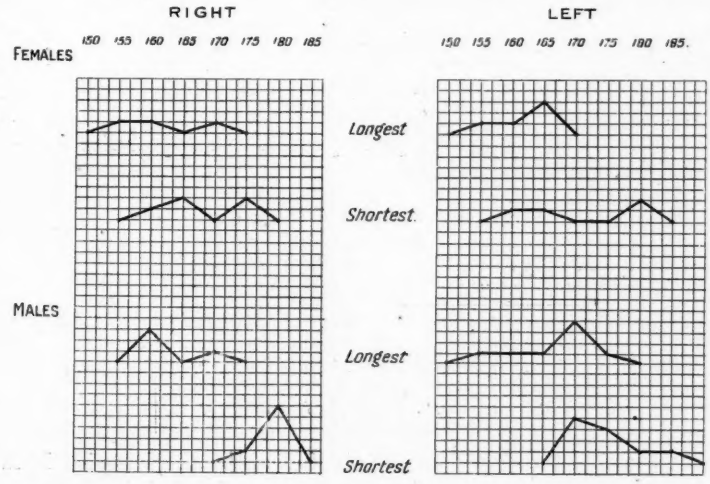

FIG. 5.—Curves to show variations in the bicondylar length index in longest and shortest bones.

degree of overlapping, yet in the main the index is higher in short bones than in long ones. It will be seen that there is less overlapping in males than in females, and that the lower indices are not seen in short bones, and vice versa.

Least Transverse Diameter of Shaft.

This is usually a little below the middle of the bone; the measurement should not be taken near the extremities. In this series the averages and range were as under:—

	Males.		Females.	
	Right.	Left.	Right.	Left.
Averages . . .	27·5 mm.	28 mm.	24·5 mm.	25 mm.
Range . . .	24–32	24–32	23–27	23–27

It will be noticed that the left bones are somewhat thicker than the right ones. Parsons found a similar condition somewhat more marked in his Rothwell series. The measurements from male specimens above quoted are a little lower than those given by Parsons as obtained from modern bones in St Thomas' and Guy's Hospital collections. The range shown in the above table is not so extreme as in the Rothwell series.

Pilastring.

The condition of femur *à pilastre* is best shown by means of an index, obtained by taking the greatest antero-posterior measurement (which may or may not be at the level of the middle of the shaft); at the same level take the transverse diameter in a plane parallel to the posterior surfaces of the condyles.

$$\frac{\text{Antero-posterior measurement} \times 100}{\text{Transverse measurement}} = \text{pilastric index.}$$

The averages in this series were—

Males.		Females.	
Right.	Left.	Right.	Left.
110·5	107·2	109·7	107

The remarkable correspondence of the indices on the left side in the two sexes might not be borne out in another series, but in Hepburn's small collection of modern Scotch femora a similar condition was found; he did not, however, draw attention to it.

When should a bone be regarded as definitely pilastred? It will be found that the condition is fairly obvious when the index exceeds 114 on the left side and 116 on the right. The curves on fig. 6 show the distribution of the variation, and also the number of markedly pilastred

bones in each group. Hepburn, not differentiating between side or sex, gives 109·3 as the average for his series; using a similar method, the average here would be 108·3. As this is somewhat misleading, the question of grouping should always be considered.

It can be seen from the curves that the left groups show a steady drop above the 114 limit, whilst the right ones develop a secondary rise above

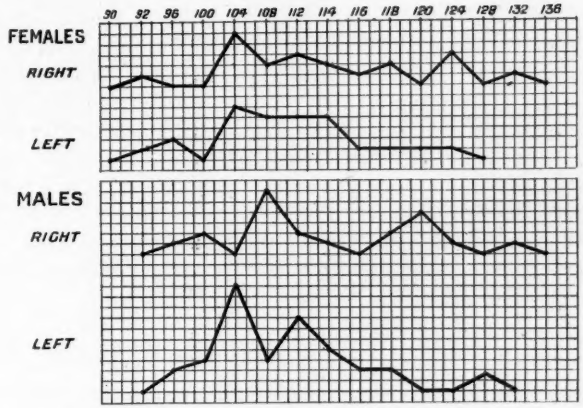

FIG. 6.—Curves to show the range of variation in the pilastric index.

the 118 level, indicating that not only is the average index higher on the latter side, but also that marked degrees of pilastring are more frequently seen there.

There is no definite relationship between the degree of pilastring and the length of the bone, high and low degrees of the former being associated with both relatively long and short specimens.

Causation of Pilastring.

Manouvrier supposed that the pilastric ridge was caused by the vasti (lateralis and medialis), just as the cranial crests in the gorilla are formed by the temporal muscles.

It may here be remarked that a specimen may show a fairly prominent linea aspera and yet not be pilastred; the linea aspera must be raised out of proportion to the width of the shaft in order to show a distinct degree of pilastring.

I will refer later to the association of pilastring and platymery, remarking only now that the two are probably *not* due to the same cause, as there is no definite correspondence in their distribution.

Now, if pilastring be dependent on, as Manouvrier stated, the degree of development of the vasti, one would expect to find a fairly definite condition of the pilastric fossæ with high and low degrees of the condition. In this series the nature of these fossæ was carefully noted in each case, and it was found whilst the medial "fossa" was usually flat or slightly rounded, the lateral one varied much in its conformation. Most frequently it was concave, but it was as often so in bones with average or relatively low indices as in those with high indices, and in the latter cases it was frequently flat, or even somewhat convex. It seems likely that the degree of prominence of the ridge may be influenced not only by the muscles at its margins but also by those attached to its lips, and here it may be said that the lateral lip is usually more prominent in well pilastred bones than it the medial one.

Platymeria.

To estimate the degree of flattening at the upper end of the shaft it is necessary to take the lowest antero-posterior measurement, usually near the small trochanter, and the transverse width at the same level.

$$\frac{\text{Antero-posterior} \times 100}{\text{Transverse}} = \text{platymeric index.}$$

Parsons has suggested that a bone should be regarded as distinctly platymeric if the index be 75 or under. In this series the averages were:—

Males.		Females.	
Right.	Left.	Right.	Left.
85·2	82·5	81·6	80·8

There thus appears to be some difference in the degree to which the condition is marked on the two sides, the left bones being flatter than the right ones. The curves on fig. 7 show that "distinct" platymeria is more common among females than among males. It is indeed one of the features recommended by Parsons for consideration in endeavouring to sex a femur, yet it is evident from the curves that a bone had not been assigned to a definite sex group on account of platymery alone. This is also shown by the comparatively small difference in the average indices of the two sexes; relatively high indices were found in both. It will be noticed that a distinct degree of platymeria is more common on the left side than on the right, and that a larger number of left-sided specimens show also a moderate degree of flattening (index between 75 and 80).

The averages in this series for the male specimens are almost exactly identical with those of Hepburn's modern Scotch femora. His female

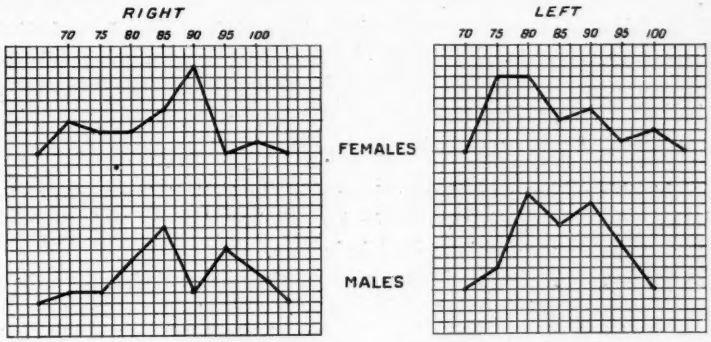

FIG. 7.—Curves to show the range of variation in the platymeric index.

averages are higher than those here given, but as he only included four female bones, his figures are scarcely reliable. Neither Hepburn or Scott referred to the sexual difference, which was first indicated by Parsons.

RELATIONSHIP BETWEEN PLATYMERIA AND PILASTRING.

If platymery be solely due to the influence of the vasti (lateralis and medialis) one would expect to see some definite relationship between it and pilastring, as was pointed out by Manouvrier, who stated that there is a close relationship between the amount of flattening in an antero-posterior direction and the flattening in a transverse direction (platymeria and pilastring): "The highest degree of the one is not, however, necessarily associated with the highest degree of the other." Hepburn agreed in the main with Manouvrier's conclusions.

In this connection one must clearly understand that a high degree of platymeria means a low index, whilst a high degree of pilastring is associated with and indicated by a high pilastric index.

The results shown in my series are not at all in conformance with the above views. There appears to be no fixed relationship between the two conditions. In each group I have selected the bones with (*a*) the most marked degree of pilastring, (*b*) the highest degree of platymery.

Females.

Right Side.—Of seven specimens with distinct pilastring (116 and over), not one showed "distinct" platymery—in the average specimens one bone

in seven should display the latter. Of the six most platymeric bones, only two showed distinct pilastring—little more than the average distribution of the condition in the group.

Left Side.—Of four bones with distinct pilastring, two showed distinct platymery; the other two had indices between 75 and 80. Of seven distinctly flattened bones, only two had evident pilastring, three others having very low indices (below 100).

Males.

Right Side.—Seven specimens showed distinct pilastring—not one had a distinct degree of platymery. Of six bones with platymeric indices of 80 and under, none showed high pilastric indices.

Left Side.—Of six distinctly platymeric pilastred bones, only two presented a platymeric index of below 80. Of twelve specimens with a platymeric index of 80 and under, only two had distinct pilastring; three others had pilastric indices of 100 and under.

A similar want of correspondence between the two conditions is seen if one takes sub-groups with low degrees of platymeria and pilastring.

The sex factor has a marked influence on the distribution and extent of platymeria, but is in abeyance in the case of pilastring. This does not support the idea of a homogeneous cause.

The Amount of Bowing.

This was estimated by Parsons' method. "The femur is laid close to the edge of a flat table in such a way that the posterior surfaces of both condyles are in contact with the table. The sliding limb of the scale is then removed, and the scale placed vertically against the edge of the table in such a manner that the fixed limb touches the point of greatest convexity of the femur about the middle of the shaft. The distance of the most convex point from the surface of the table is then shown on the scale. By keeping the scale pressed against the table edge any deviation from the vertical is prevented."

As the mere amount of bowing would mean little unless taken in conjunction with the length of the femur, he advocates the use of an index, "obtained by dividing the oblique length into the amount of bowing multiplied by 100; in this way the greater the index the greater is the bowing compared with the length of the femur." To bring this index into line with the head length and bicondylar length indices it is more convenient to multiply the amount of bowing by 1000 in place of 100, and so obtain a whole number.

The amount of bowing itself showed a close parallelism on the two sides.

Females.		Males.	
Right.	Left.	Right.	Left.
56 mm.	56 mm.	60 mm.	58 mm.

The sexual difference is small, and may be obliterated if the relative lengths be considered as in the index.

INDEX OF BOWING—AVERAGES.

Females.		Males.	
Right.	Left.	Right.	Left.
138	136	134	136

I need only quote two examples to show how misleading the mere amount of bowing would be if it were taken as indicating the degree of bowing, and how necessary it is that the length of the specimen should be considered, as it is in the index of bowing.

Two male bones, each with an index of 141, showed an amount of bowing of 72 mm. and 57 mm. respectively; two other bones with an amount of bowing of 61 mm. showed indices of 144 and 163 respectively.

From fig. 8 it will be seen that, on the whole, short bones are more curved than long ones. Sex and side appear to have little influence on the degree of curvature, the slightly higher index in females shown above being due to the shorter length of these groups. There is no definite relationship between the degree of bowing, degree of pilastring, and degree of platymery, marked conditions of the latter two being found with either high or low indices of bowing.

The question sometimes arises as to the number of specimens necessary to enable one to form an opinion as to the average characteristics. In order to ascertain the size of the group necessary I divided these bones into divisions of 10, 20, and 50 as they had come to hand when first measured. Only the indices of platymery, pilastring, and bowing were considered, as measurements of head—length, width, etc.—depend so much on the relative proportions of the two sexes in each group. The results set out below

indicate that no group of less than twenty can be used to draw conclusions from, and that a group of fifty would be more desirable. The maximum

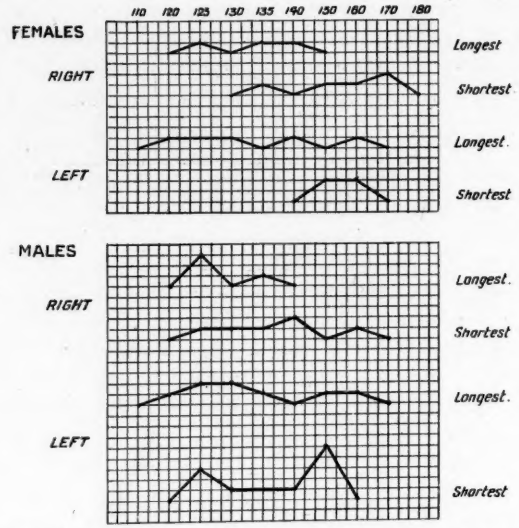

FIG. 8.—Curves to show the influence of length on the index of bowing.

error with groups of 20 is only 2·5 per cent.; with groups of 50 it is reduced to 1·4 per cent.

Number in group.	Index of bowing.	Platymeric index.	Pilastric index.
10	Error does not exceed 3·5 per cent. Average error 1·7 per cent.	Greatest error 5 per cent. Average error 3 per cent.	Greatest error 5 per cent. Average error 2 cent.
20	Greatest error 2·2 per cent. Average error 1 per cent.	Greatest error 2·6 per cent. Average error 1·5 per cent.	Greatest error 1·5 per cent. Average error 0·6 per cent.
50	Greatest error 1·4 per cent. Average error 1·4 per cent.	Greatest error 1·25 per cent. Average error 0·8 per cent.	Greatest error 0·6 per cent. Average error 0·6 per cent.

SUMMARY.

1. The average length of the bones in each group resemble those in Parsons' Rothwell series so closely, that we may assume there has been little or no change in stature since the Middle Ages. It would be interesting to know if the remarkable differences between the right and left sides in males is borne out by a fairly large series of known pairs.

2. The sex distribution as regards diameter of head seems to vary within somewhat narrower limits than Parsons and Dwight thought, viz. bones with a measurement of less than 44 mm. are usually females, those over 46 are usually males.

3. Short bones have relatively larger extremities than long ones. Profound!

4. There is more variation in the diameter of the head than of the bicondylar width on the two sides.

5. Left femora have somewhat broader shafts than their fellows.

6. Pilastring is fairly common nowadays, and may be said to be distinct if the index be over 114 on the left side and 116 on the right. The latter are not only more pilastred in the average, but also show a larger percentage of distinctly pilastred bones than does the left side.

7. There is a sexual influence in the degree of platymery, but no difference between the two limbs.

8. The degree of platymery bears no definite relationship to that of pilastring, so the two are probably not due to the same cause.

9. Generally speaking, short bones are more bowed than long ones.

10. There is no definite inter-relationship between bowing, platymery, and pilastring.

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[TABLE.

TABLE No. I. (A). RIGHT FEMALE SPECIMENS (20).

Number in series.	Diameter of head.	Bicondylar width.	Oblique length.	Maximum length.	Least transverse diameter of shaft.	Head length index.	Amount of bowing.	Index of bowing.	Platymeric index.	Pilastric index.
	mm.	mm.	cm.	cm.	mm.		mm.			
III.	40	67	40·8	41·1	25	97·3	55	134	86·6	116
X.	45	69	41·8	41·85	26	107·4	59	155	83·8	112·5
XI.	41	64	40·8	40·9	25	100·2	53	129	76·3	120
XIV.	40	66	37·3	37·4	24	106·9	57	152	76·4	120·8
XXI.	41	66	39·8	40	24	102·5	56	140	85·7	108·2
XXVI.	40	65	41·4	41·8	22	95·7	54	125	85·7	116·6
XLIV.	45·5	69	43·5	43·7	26	103	61	140	85·2	111 0
XLV.	41	71	41·2	41	24	100	55	137	73·5	104
XLIX.	41	73	43·4	43·8	25	93·6	59	135	75	115·3
LVIII.	44	70	42·9	43·2	25	101·8	60	139	87	103·4
LIX.	37·5	60	37·9	38·1	24	98·4	51	134	88·8	101
LX.	40	68	39·7	40·1	22	99·6	51	128	90	122·7
LXI.	43	69	40·2	40·7	24	105·6	53	131	70	104
LXIV.	41	64	38·6	38·9	26	105·3	56	145	80·3	92·3
LXX.	44	70	43·1	43·3	27	101·6	54	125	65·7	100
LXXVI.	44	67	44·6	45·2	26	97·2	56	125	69·6	100
LXXVII.	45	73	41	42·3	25	106·3	59	130	82·8	100
LXXIX.	40	66	37·7	38	23	105·2	62	164	100	128
LXXXVII.	45	72	42·1	42·3	25	106·3	61	144	84·3	103
XC.	40	62	37·4	38	24	105·2	61	163	86·6	112

TABLE No. I. (B). LEFT FEMALE SPECIMENS (24).

Number in series.	Diameter of head.	Bicondylar width.	Oblique length.	Maximum length.	Least transverse diameter of shaft.	Head length index.	Amount of bowing.	Index of bowing.	Platymeric index.	Pilastric index.
	mm.	mm.	cm.	cm.	mm.		mm.			
VIII.	42	66	41·5	41·7	25	100·7	58	139	86·2	103·1
IX.	40	61	38·3	38·5	23	103·8	59	155	82·1	112·5
XIII.	44	73	43	42·2	24	104·2	57	132	97	108·2
XVII.	40	68	41·1	41·4	26	96·6	54	131	87	107·6
XXV.	43	69	43·1	43·2	27	99·5	54	125	78	100
XXVII.	40	63	38·7	39·3	26	101·7	60	155	83·3	107·6
XXX.	42	70	41·1	41·4	27	101·4	53	129	83·8	100
XXXII.	37	64	40·1	40·4	25	91·5	55	135	73·3	108
XXXIV.	44	70	42·9	43·1	23	102	53	123	70·3	117·3
XXXV.	40	64	39·8	40·1	24	99·7	56	143	75·8	112·5
XLI.	42	66	40·4	40·9	26	102·6	56	138	75	112
XLII.	41	65	41·4	41·45	23	98·9	57	137	78·5	114
L.	43	67	40·3	40·5	26	106·1	56	138	78·1	100
LII.	41	67	37·9	38	24	108	54	142	75	92·2
LXII.	41	66	41·7	42	26	97·6	54	129	86·2	100
LXIII.	46	69	42	42·3	26	108·7	57	135	77·4	111·1
LXXII.	43	74	42·4	42·6	26	100·9	57	134	93·5	107·6
LXXVIII.	44	70	45	45·1	29	97·5	60	111	86·2	112·5
LXXXII.	42	70	46·1	46·4	24	90·5	60	130	78·1	120
LXXXV.	40	67	42·2	42·5	26	94	57	135	96·5	107·6
XCI.	37	64	42·2	42·2	22	87	48	113	72·4	95·6
XCII.	44	73	44·7	44·8	26	98	63	140	80	110·7
XCV.	44	70	43·5	43·6	25	100·9	66	152	72·7	119·2
XCVI.	37	63	35·8	36·2	25	100·2	51	142	72·4	87·5

TABLE No. I. (C). RIGHT MALE SPECIMENS (21).

Number in series.	Diameter of head.	Bicondylar width.	Oblique length.	Maximum length.	Least transverse diameter of shaft.	Head length index.	Amount of bowing.	Index of bowing.	Platymeric index.	Pilastric index.
	mm.	mm.	cm.	cm.	mm.		mm.			
IV.	51	74	44·8	45·4	24	110·2	57	127	96·5	112·5
VI.	45	76	43·5	44	26	102·2	54	125	93	118·5
VII.	50	80	47·6	47·8	30	104·6	58	121	74·3	103·1
XXVIII.	46	72	40·3	40·4	32	113	63	156	78·3	106·9
XXIX.	51	85	43·9	44·4	26	104·8	63	143	80	107·4
XXXIII.	51	80	51·5	51·6	30	98·8	63	122	84·2	120
XXXVI.	46	82	46·3	46·2	31	99·5	63	136	93	106·4
XLVI.	43	76	43	43·1	25	99·7	55	127	90·6	118·5
LI.	45	75	42·4	42·6	25	105·6	58	139	80	108
LV.	47	74	43 8	43·9	27	107	61	139	84·3	118·5
LVI.	51	78	45·6	46·2	29	110·4	66	144	100	128·5
LXVIII.	51	77	42·9	43·1	28	118·2	62	129	83·3	117·2
LXXIII.	46	75	47·3	47·6	26	96·6	62	131	90·3	118·5
LXXIV.	50	79	44·7	44·9	28	111·3	58	129	76·4	96·4
LXXXI.	51	82	51·4	51·6	30	98·8	63	122	69·4	93·9
LXXXVI.	45	75	44·6	44·8	26	100·4	57	127	89·2	96·1
LXXXVIII.	48	78	43·9	44·6	26	107·6	63	143	82·3	107·4
LXXXIX.	46	75	45·5	45·9	27	100·2	60	131	84·3	107
XCIV.	50	81	45·5	45·7	27	109·4	68	149	82·3	116·6
XCVII.	49	77	45·6	45·8	28	107	59	129	84·2	110·7
XCIX.	45	75	42·3	42·5	25	105·8	59	139	93·3	106·5

TABLE No. I. (D). LEFT MALE SPECIMENS.

Number in series.	Diameter of head.	Bicondylar width.	Oblique length.	Maximum length.	Least transverse diameter of shaft.	Head length index.	Amount of bowing.	Index of bowing.	Platymeric index.	Pilastric index.
	mm.	mm.	cm.	cm.	mm.		mm.			
I.	49	77	44·9	45·1	28	108·7	59	131	90	110·3
II.	48	80	47·4	47·8	28	100·4	63	132	87	110·3
V.	51	85	46·7	46·9	30	108·7	56	119	75	103·3
XII.	55	82	50·1	50·4	30	109·1	63	125	77·7	100
XV.	48	82	46	46·5	28	103·2	65	141	80	117·2
XVI.	45	73	42·9	43	26	104·6	53	123	92·3	114·6
XVIII.	46	73	43·6	43 9	27	104·7	54	123	81·8	111
XIX.	49	80	45	45·5	27	107·6	61	135	75·6	111·1
XX.	55	80	52·1	52·3	30	105·1	59	113	79·4	113·3
XXII.	45	71	46·5	46·7	30	96·3	60	129	74·2	103
XXIII.	47	78	44·5	44·5	27	105·4	53	118	81·8	103
XXIV.	46	73	42·3	42·8	26	107·4	57	141	74·2	100
XXX.	44	73	42·8	43·4	28	101·3	54	125	82·5	103
XXXI.	49	80	45·5	45·8	31	106·9	60	131	80	107
XXXVII.	47	75	41·9	42·5	26	110·5	54	129	84·8	100

TABLE No. I. (D). LEFT MALE SPECIMENS—*continued.*

Number in series.	Diameter of head.	Bicondylar width.	Oblique length.	Maximum length.	Least transverse diameter of shaft.	Head length index.	Amount of bowing.	Index of bowing.	Platymeric index.	Pilastric index.
	mm.	mm.	cm.	cm.	mm.		mm.			
XXXIX.	45	72	43·4	43·5	28	103·4	62	142	81·2	93·3
XL.	45	76	41·5	41·6	24	108·1	56	135	90·3	96·8
XLIII.	47	75	46·8	47·3	28	99·3	59	125	90·6	116·6
XLVII.	47	76	44·6	46·4	31	101·2	60	134	83·8	103
XLVIII.	46	77	45·6	45·8	27	100·4	61	133	69·4	111·5
LII.	47	76	44	44·1	28	106·4	56	127	85·2	103
LIV.	47	79	43·1	43·1	29	109·4	61	141	85·2	110
LVII.	57	80	46·7	46·8	30	121·7	70	149	91·1	113·3
LXV.	51	80	46·8	47·3	28	107·8	69	147	76·4	96·4
LXVI.	51	75	44·6	44·9	27	113·5	60	134	81·8	103
LXVII.	46	73	41	41	27	112·2	60	146	87·5	115
LXIX.	53	81	45·2	45·5	28	116·4	54	119	87·8	99
LXXII.	48	71	41·9	42·2	25	113·7	59	140	86·2	104
LXXV.	47	80	47·8	48	28	97·9	62	129	75·6	117·2
LXXX.	51	76	48·2	48·4	27	105 3	76	153	87·5	125
LXXXIII.	56	85	50·5	50·8	30	110·2	72	142	93·9	109·6
LXXXIV.	49	80	48·1	48·5	27	101·3	63	130	87·5	113·7
XCIII.	51	84	48·7	48·6	32	105	59	121	76·3	93·9
XCVIII.	47	72	45·7	46·1	28	102	66	144	76·4	113·7
C.	47	77	43·5	43·8	28	107·3	62	142	77·1	106·8

TABLE II.—AVERAGE MEASUREMENTS AND INDICES.

Sex side.	Diameter of head.	Bicondylar width.	Oblique length.	Maximum length.	Least transverse diameter of shaft.	Head length index.	Bicondylar length index.	Amount of bowing.	Index of bowing.	Platymeric index.	Pilastric index.
	mm.	mm.	cm.	cm.	mm.			mm.			
Females, right	42	67·5	41·1	41·4	24·5	102·5	165	56	138	81·6	109·7
Females, left .	41·5	67·5	41·4	41·6	25·1	100·2	162	56	136	80·8	107
Males, right .	48	77	45·0	45·3	27·5	105·5	171	60	134	85·2	110·5
Males, left . .	49·6	76·6	45·7	46·0	28	106·4	170	58	136	82·5	107·2

THE MUSCLES RELATED TO THE BRANCHIAL ARCHES IN RAIA CLAVATA.

By EDWARD PHELPS ALLIS, Junr., *Menton, France.*

TIESING, in 1896, described the muscles related to the visceral arches in one of the Selachii, *Mustelus lævis*, and in three of the Batoidei—*Raia clavata*, *Rhinobatus annulatus*, and *Torpedo occellata*. In these descriptions Tiesing followed Vetter (1874) in giving to the musculus constrictor superficialis of each visceral arch the number of the arch to which he considered it to belong, beginning with the mandibular arch as No. 1. In Mustelus, the constrictores superficiales of the branchial arches, as identified by Tiesing and numbered according to this method, each lies, as it does in Vetter's descriptions, posterior to the visceral cleft that lies next anterior to the arch that bears the same number as the constrictor. In the Batoidei, on the contrary, each branchial constrictor, as identified and numbered by Tiesing, lies anterior to that visceral cleft, and hence actually in the branchial arch next anterior to the one to which it is assigned; and there are seven of these constrictores in these fishes, instead of six, as in those of the Selachii that have the same number of gill clefts. The so-called seventh constrictor is assigned to the fourth vagus arch, an arch in which there is said to be, in these fishes, no musculus interbranchialis, and, in the Selachii, neither interbranchialis nor constrictor superficialis.

Marion, in a later work (1905), accepted and followed, without question, Tiesing's identification of these muscles in the Batoidei.

The constrictores superficiales of the branchial arches of the Batoidei, as identified and numbered by these two authors, thus present not only certain marked departures from the conditions found in the Selachii, but also certain evident abnormalities. This was first brought to my attention while I was engaged on my recent work on the muscles related to the branchial arches of the gnathostome fishes, and I there stated (Allis, 1917, p. 343) my conviction that there must be some error in the descriptions of these muscles. This has led me, since the work above referred to was sent to press, to have these muscles carefully examined in two adult specimens of *Raia clavata* and one of *Raia radiata*, and they are here all redescribed, and their innervation, as I find it, given. The prebranchial muscles related to the hyal and mandibular arches, as found in *Raia clavata*, are

also summarily considered, but I have not attempted to determine their innervation, excepting only that of the depressor mandibularis, the innervation given by Tiesing and Luther (1909) being accepted as correct.

The preliminary dissections relating to this work were all made by my assistant, Mr John Henry, and were limited to *Raia clavata*. The drawings, and the dissections from which they were made, are by Mr Jujiro Nomura. Figs. 1, 2, and 6 are of *Raia radiata*, the others all of *Raia clavata*. The descriptions refer to *Raia clavata* unless otherwise definitely stated, and Tiesing's nomenclature has been employed, as far as possible.

The m. adductor mandibulæ medialis is practically as described by Tiesing, but I find it definitely continuous, in its anterior portion, with the adductor mandibulæ lateralis I., as Luther (1909) says that it also was in certain of the Batoidei examined by him. The muscle, as it passes from the upper to the lower jaw, is flat and wide, and bounds the deep angle of the gape of the mouth, as Luther shows it in Myliobatis.

The m. adductor mandibulæ lateralis I. is also as described by Tiesing. It runs posteriorly in a nearly straight line across the angle of the gape of the jaws, the adductor mandibulæ medialis appearing to be an offshoot of it. These two muscles, together, apparently represent the primitive adductor of the arch, and correspond to the adductor muscles of the branchial arches.

The m. adductor mandibulæ lateralis II. arises on a ligamentous formation that is strongly attached to the abdental edge of the palato-quadrate, but that is continued, as a strong ligamentous band, across the internal surface of that cartilage and then across the angle of the gape of the jaws to be inserted on the mandibula; this being practically as Luther describes it. The muscle, near its origin, bulges anteriorly, its fibres running at first antero-laterally and then curving posteriorly across the external surface of the palato-quadrate, and all of its fibres are inserted either on the internal surface of a tough fascia that covers the ventral surface of the muscle, or on an aponeurosis, developed in relation to that fascia, that extends transversely across the muscle in the line prolonged of the opening of the mouth. Posterior to this aponeurosis most of the fibres of the muscle take their origins from the aponeurosis and from the internal surface of the ventral fascia, but a considerable part of them arise from the external surface of that fascia. The former fibres lie mesial to the latter ones, and, running posteriorly, are inserted on the abdental edge of the mandibula, the line of insertion of these fibres lying not far from the point of origin of the ligamentous band related to the anterior end of the muscle. This part of the muscle thus in part

encircles the mandibles, instead of extending between them, and hence must act as a compressor rather than an adductor of them. Those fibres of the muscle that have their origins on the external surface of the fascia

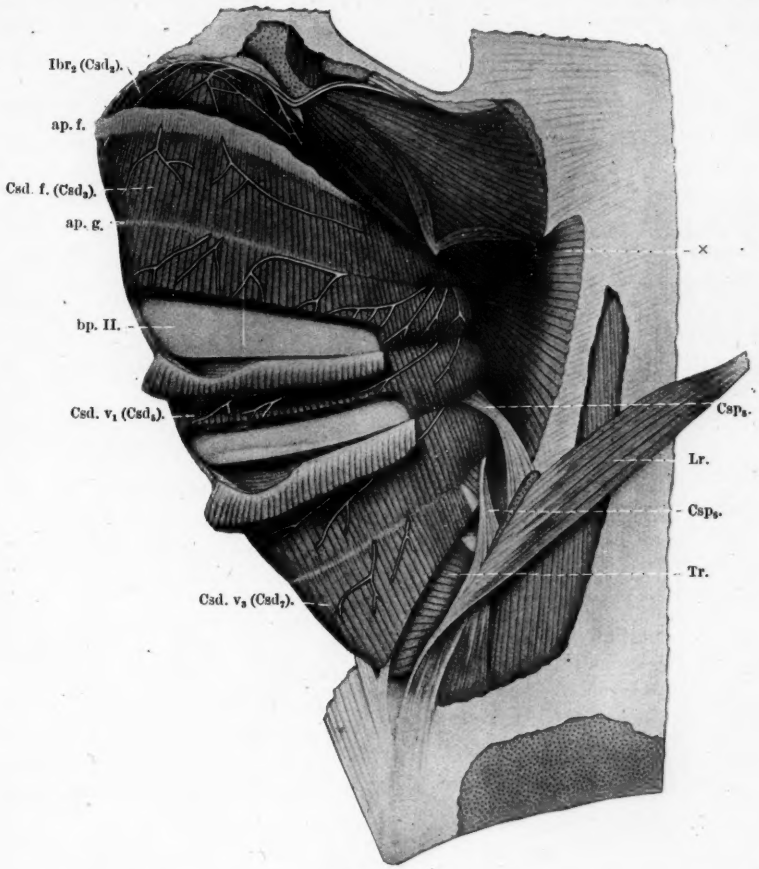

FIG. 1. ×1½.

on the ventral surface of the muscle form the postero-lateral portion of it, and, running posteriorly, postero-laterally, and even laterally, are inserted on the palato-quadrate near its articular end. These fibres, although definitely separate, at their insertions, from the other fibres of the muscle, are elsewhere directly continuous with them, the two sets

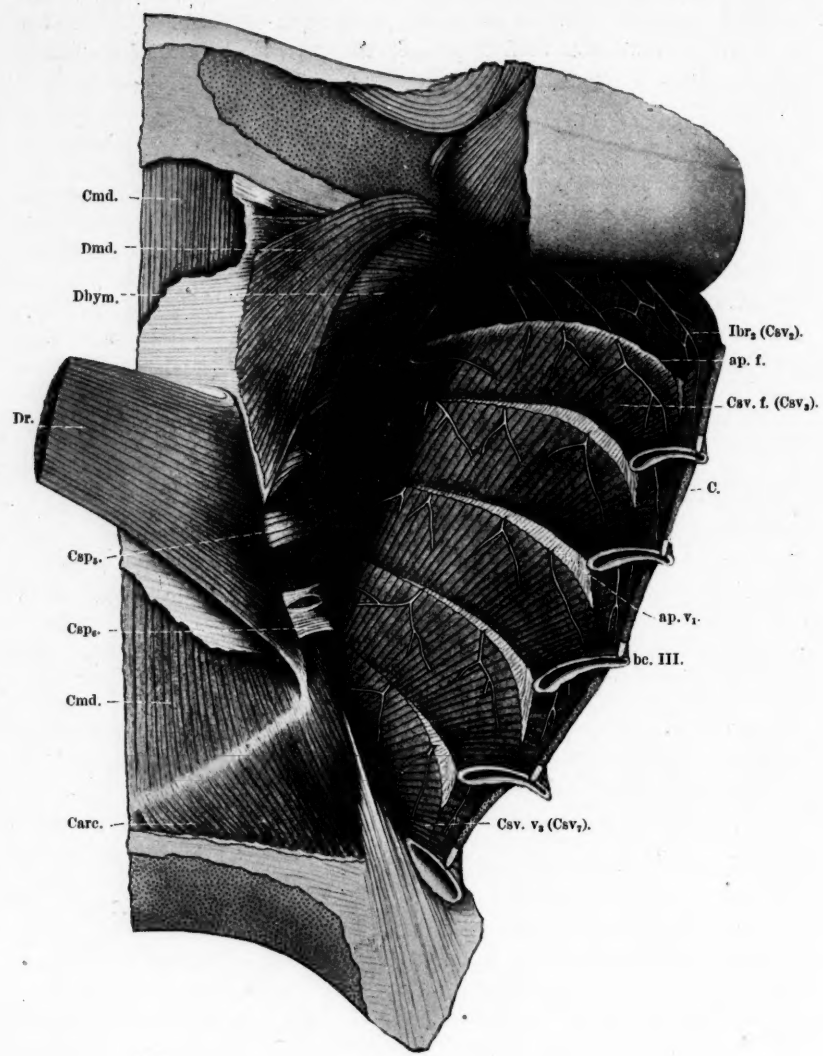

FIG. 2. $\times 1\frac{1}{2}$.

of fibres forming a single continuous muscle which is partly separated into two parts by a furrow on its external surface. The fibres that are inserted on the palato-quadrate I do not find described by either Tiesing, Marion (1905), or Luther, but they form an important part of the muscle in all my specimens, and they, together with the musculus superioris II. and parts, described immediately below, of the fascia on levator labii the ventral surface of the adductor, quite certainly represent the muscle Addγ of Vetter's descriptions of the Selachii; as comparison with Luther's descriptions of this latter muscle in Heptanchus will make evident.

The fascia that covers the ventral surface of this division of the adductor is a tough membrane which has posterior, anterior, and antero-lateral extensions. Posteriorly the fascia extends over the posterior edge of those fibres that are inserted on the mandibula, but penetrates the muscle between those fibres and the fibres that are inserted on the palato-quadrate. That part of the fascia that extends posteriorly over the posterior edge of the muscle in part vanishes on its posterior surface, but is in part continued as a fibrous band, of variable form, that has its insertion on the anterior surface of the muscle Cs_2 of Tiesing's descriptions, near the middle of the dorso-ventral length of that muscle and not far from its proximal, deeper edge. The mesial edge of the fascia runs into the subdermal tissues at the angle of the gape of the mouth, and is there continuous with the fascia related to the labial cartilages. At about the posterior third of its mesial edge the fascia gives origin to a stout tendon which runs mesially across the external surfaces of the musculi adductor mandibulæ lateralis I. and depressor mandibularis, and then internal to the musculus coraco-mandibularis, there lying in the membrane that separates the latter muscle from the musculus coraco-hyoideus. In that membrane it continues mesially, and is continuous, in the median line, with its fellow of the opposite side of the head. Anteriorly, the fascia separates into two parts. The lateral portion turns dorso-anteriorly over the lateral edge of the muscle, crosses the lateral surface of that muscle and then that of the levator labii superioris II., and reaches the dorsal surface of the latter muscle. There it turns antero-mesially and is inserted on the dorso-posterior surface of the nasal capsule, this part of the fascia being the levator labii superioris V. of Tiesing's fig. 13, pl. 7. The mesial portion of the fascia is slightly thickened along its lateral edge, and from that thickened portion, which lies along the antero-lateral edge of the ventral surface of the adductor, numerous tendinous strings, or a tendinous band, extend to the ventro-posterior edge of the lateral ethmoidal process (cartilago-parethmoidalis, Luther). These tendons are

shown by Tiesing in one of his figures of this fish (fig. 11, pl. 6), and are there called by him the levator labii superioris V.; but the tendinous band shown in that figure is not the same as the one shown in his fig. 13, pl. 7, which, as just above explained, is also called the levator labii superioris V. Beyond the line of origin of these tendons the main fascia turns upward over the rounded anterior edge of the adductor mandibulæ lateralis II., internal to the levator labii superioris IV., and then becomes in part a broad band which, running dorso-mesially, is inserted on the dorso-posterior surface of the nasal capsule. This band gives insertion, along the dorsal portion of its anterior surface, to certain fibres of the musculus levator labii superioris III., and it lies closely against a stout membrane that here covers the posterior surface of the nasal capsule, this latter membrane giving insertion to the musculus levator labii superioris IV.

The m. levator labii superioris I. is as described by Tiesing; and Luther (1909, p. 46) considers this muscle alone, of the several levatores described by Tiesing, to represent the levator labii superioris of the Selachii (m. præorbitalis, Luther).

The m. levator labii superioris II. is a thick muscle which arises on the mandibula by a large tendinous end which lies internal (dorsal) both to the adductor mandibulæ lateralis I. and to that part of the adductor mandibulæ lateralis II. that is inserted on the mandibula, the point of attachment of the tendon lying anterior (oral) to the points of insertion of the adductores. The muscle runs at first dorsally, or dorso-antero-laterally, internal and mesial to the adductor mandibulæ lateralis II., this being approximately as this muscle is shown in Tiesing's fig. 15, pl. 7, of Rhinobatus, but not at all as it is shown in his figure of Raia. A few of the fibres of the muscle are inserted on the internal surface of that portion of the large fascia related to the adductor that gives origin, on its external surface, to those fibres of the adductor mandibulæ lateralis II. that have their insertions on the palato-quadrate. The levator then receives a bundle of fibres, of variable importance, from that part of the adductor mandibulæ lateralis II. that is inserted on the mandibula, and, turning anteriorly, is inserted on the internal surface of what I have above described as the antero-lateral extension of the large fascia on the ventral surface of the adductor mandibulæ lateralis II., its fibres crossing the dorso-lateral surface of the bulging anterior portion of the latter muscle. Most of the fibres of the levator cross, at a considerable angle, that terminal portion of the antero-lateral extension of the large fascia that, as above explained, has its insertion on the posterior surface of the nasal capsule, but a part of them are inserted on the base of that portion of the fascia, that part of the fascia thus being, in part, the tendon of insertion of the levator. Tiesing and Marion both give this as

the sole insertion (origin) of the levator, and it apparently has so definitely become in Rhinobatus, as shown in Tiesing's fig. 15, pl. 7.

The m. levator labii superioris II. is considered by Luther to represent that part of the adductor mandibulæ of the Selachii that Vetter described as the muscle Addγ, with which conclusion I fully agree, excepting that, as already stated, I would include in the muscle Addγ those fibres of the adductor mandibulæ lateralis II. that have their insertions on the palato-quadrate. The long tendinous anterior portions of the muscle Addγ of the Selachii are represented in portions of the fascia on which, in the Batoidei, the two muscles above referred to are inserted. This muscle Addγ, so constituted, I consider to represent the musculus interbranchialis of the mandibular arch, the musculus adductor mandibulæ lateralis II. being that part of the constrictor superficialis of the mandibular arch that lies distal (external) to the interbranchialis and is represented, in the Selachii, by the so-called dorso-ventral fibres of the constrictores superficiales. This distal portion of the primitive constrictor has here slipped over the distal edge of the musculus interbranchialis on to the anterior surface of that muscle, and also on to that surface of the cartilaginous bar of the mandibular arch, and, by its contraction, it compresses the mandibles and so increases the effect of the primary adductor of the arch, the latter muscle having been cut out of the middle of the dorso-ventral length of the proximal fibres of the primitive constrictor. The interbranchiales of the branchial arches of this fish have their origins both on the epal and the ceratal elements of their respective arches, and they in part run outward perpendicularly to those elements, as will be later described, this accounting for the course of the fibres in the mandibular arch. The fact that it is in this fish, and hence probably also in the Selachii, only those fibres of the constrictor that lie distal to the interbranchialis that thus slip over on to the anterior surface of the arch, to there be added to the primary adductor, would then account for the varying relations of the definitive adductor of the Selachii to the nervus trigeminus, that nerve sometimes lying on the external surface of that muscle and sometimes between its superficial and deeper portions.

The m. levator labii superioris III. is as described by Tiesing, and its relations to the levator labii superioris IV. would seem to indicate that it is a differentiated portion of that muscle.

The m. levator labii superioris IV. is a thin band of muscle fibres which arises from the external (ventral) surface of the large fascia on the ventral surface of the adductor mandibulæ lateralis II. and, running antero-dorso-mesially in a curved course, is inserted on the dorso-posterior surface of the nasal capsule.

The so-called m. levator labii superioris V. of Tiesing's descriptions is,

as already stated, simply part of the large fascia that covers the ventral surface of the adductor mandibulæ lateralis II.

The muscle Csd_1 is as described by Tiesing.

The m. levator maxillæ superioris arises by two tendons, as described by Tiesing, but I find the lateral edge of the deeper, inferior one of these two parts of the muscle attached by ligamentous tissues to the lateral end of the mandibula. In one of the two specimens examined, but not in the other, this ligament formed the lateral prolongation of an aponeurosis that partly crossed the muscle transversely. In this same specimen the ventral surface of the inferior muscle was crossed transversely by muscle fibres and also by numerous fibrous strings, these strings forming, mesial to the muscle, a fascia which was attached to the lateral edge of the trabecular region of the cranium.

The m. depressor mandibularis was, in one of my two specimens of *Raia clavata*, a single muscle such as is described by Tiesing and also by Marion. In the other specimen the muscle was double on each side of the head, one muscle lying immediately antero-mesial to the other, and, on one side of the head, partly internal to it. Both muscles arise from the lateral edge, or ventral surface, of the large median fascia that ensheaths the musculus coraco-mandibularis, and both are inserted on the mandibula, the anterior muscle by a tendinous end, but the posterior muscle directly on the cartilage, the muscle bundles of this latter muscle being directly continuous with those of the musculus adductor mandibulæ lateralis I. Tiesing says that this muscle is innervated by the nervus facialis; Marion calls it the posterior part of the constrictor of the mandibular arch, which would indicate that he found it innervated by the nervus trigeminus. I find both parts of the muscle innervated in *Raia clavata* by a branch of the nervus trigeminus, and two strictly similar muscles in Rhynchobatus are included by Luther among those innervated by the same nerve.

A small musculus intermandibularis, similar to the muscle described by Marion in *Raia erinacea* as the muscle Csv_1, was found in one of my two specimens but not in the other. Luther describes, in *Raia clavata*, a few feeble muscle fibres which he considers to represent the intermandibularis, but these fibres did not reach the median line.

The muscle Csd_1 and the levator maxillæ superioris have certainly both been differentiated from the dorsal end of the primitive constrictor of the mandibular arch, and it would seem as if the levator maxillæ superioris must be formed from those dorsal portions of the proximal fibres of the primitive constrictor that were left after the primitive adductor was cut out of them, the muscle Csd_1 representing corresponding portions of the more distal fibres of the constrictor. The levator maxillæ superioris would

then be the serial homologue of the arcuales and interarcuales of the branchial arches, which Dohrn (1884) says are differentiated from the proximal fibres of their respective arches. The depressor mandibularis and the intermandibularis have been differentiated from the ventral end of the primitive constrictor, the depressor mandibularis, because of the continuity of its fibres with those of the adductor mandibulæ lateralis I., quite certainly from the proximal fibres of this part of the constrictor.

The m. levator hyomandibularis, levator rostri, and depressor rostri are as described by Tiesing, the levator hyomandibularis arising from the cranial wall immediately dorsal to the muscle Csd_1. In each of my two specimens of *Raia clavata* the levator hyomandibularis is connected by a small bundle, or a few fibres, with a part of the muscle Csd_2 of Tiesing's and Marion's descriptions. On both sides of the one specimen of *Raia radiata* that was examined, three little bands of muscle fibres had separated from the muscle and, running together to a point, were attached to tissues related to the thymus. These little bands were not found in *Raia clavata*.

The m. depressor hyomandibularis, excepting only a small anterior bundle, arises from the lateral edge of the large median ventral fascia, internal to the depressor mandibularis. The one bundle of the muscle that does not have this origin arose, in one of my two specimens of *Raia clavata*, by a long tendon from the ventral surface of the mandibula of the opposite side of the head, not far from the symphysis, the tendon of the muscle of one side of the head traversing, as it crossed the median line, a perforation of the tendon of the other side. In the other specimen the tendons of the muscles of opposite sides were directly continuous with each other, and there was no insertion on the mandibulæ. As in the case of the levator hyomandibularis, this depressor muscle is connected by a small bundle, or by a few fibres, with a part of the muscle Csv_2 of Tiesing's and Marion's descriptions.

The muscles related to the branchial basket may now be considered, and these muscles form a group that is wholly separate and distinct from those above described, excepting only in that, as just above explained, the muscle Cs_2 of Tiesing's and Marion's descriptions is connected by a few fibres both with the levator and the depressor hyomandibularis.

The gill-pouches on either side of the head of *Raia clavata* have practically vertical anterior and posterior walls and horizontal dorsal and ventral walls, this being simply an exaggeration of the conditions described by me in Scyllium and Mustelus (Allis, 1917), in which latter fishes the anterior wall of each gill-pouch runs, from within, at first postero-externally and then curves posteriorly parallel to the external surface of the body. The lateral walls of the pouches of Raia are vertical in position,

but slightly concave because of the pressure against them of the tissues related to the lateral fin. The anterior pouch of the series lies between the facialis and glossopharyngeus arches and is nearly transverse in position, inclining slightly anteriorly. The four remaining pouches lie between each succeeding pair of branchial arches, from the glossopharyngeus to the fourth vagus, and incline successively more and more posteriorly. The five pouches, together, thus form a series of box-like structures placed side by side and wider at their lateral than at their mesial ends, each box straddling the space between two adjacent branchial bars and being separated from its neighbour on either side by the related branchial diaphragm. The internal, or pharyngeal opening of each pouch is large. The external opening is small, and lies at the lateral end of the ventral wall of the pouch, close against its posterior wall.

The four branchial diaphragms that lie between the five branchial pouches, excluding the anterior and posterior walls of the branchial basket, are wedge-shaped, being thick at their internal edges and becoming rapidly thinner externally. The branchial rays form the posterior surface of the wedge, and lie against the anterior wall of the next posterior gill-pouch, all of them extending to the outer edge of that pouch. There, all of them, excepting the middle ray of the series, turn abruptly posteriorly, practically at right angles, and, becoming more or less flattened and enlarged, fuse in part with each other, as is well shown in Foote's (1897) figure of *Raia radiata*. These flattened outer ends of the rays lie in the dorsal and ventral walls of the next posterior gill-pouch, and extend nearly to the posterior edges of those walls, the bent outer end of the lateral one of the dorsal rays lying over the angle between the dorsal and lateral walls of the pouch, and the corresponding end of the lateral one of the ventral series lying over the angle between the ventral and lateral walls, the bent and flattened outer ends of the rays thus forming a strong support to the dorsal and ventral walls of the pouch. Between the lateral ones of these two series of rays there is but a single ray, the middle one of the entire series, the base of this ray being contiguous with that of the adjacent ray on either side, but its outer end being separated from the outer end of each of those rays by a considerable interval. This middle ray of the series in each arch is not bent at its outer end, as the other rays all are, being straight throughout its entire length. It is directed laterally and slightly ventrally, and extends slightly beyond the level of the lateral wall of the gill-pouch next posterior to it, there being imbedded in the anterior edge of that wall, and, pushing it outward, forming a slight rounded protuberance in the wall. Its distal half has, in each arch, cut through the musculus interbranchialis of the arch, and is exposed on the

anterior surface of that muscle, its proximal portion being covered by an aponeurotic line; and it and this aponeurotic line together have the position of the black line shown in Marion's fig. 12 of *Raia erinacea*, and there apparently giving insertion to the fibres of the interbranchialis. What this black line is intended to represent I am unable to determine. It is shown by Marion as a branch of a main black line that follows the curve of the branchial bar of the arch, that lies along the anterior surface of the proximal ends of the fibres of the musculus interbranchialis, and that sends several smaller branches outward obliquely across the fibres of that muscle. The main black line cannot represent either of the main blood-vessels of the arch, for both those vessels lie posterior to the interbranchialis, and if

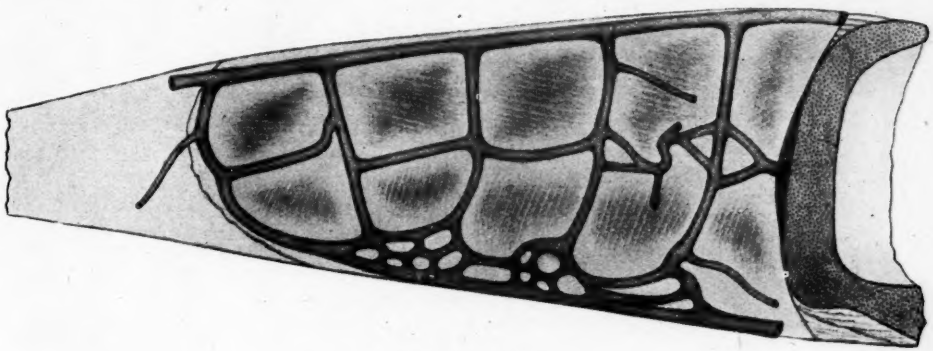

FIG. 3. ×1½.

it is intended to represent the nerve of the arch, the line that gives insertion to the fibres of the interbranchialis does not exist as a branch of the nerve.

The lateral fin of either side lies along the lateral surface of the branchial basket, and it and the related tissues are easily removed, leaving a clean surface of separation. When it has been removed there is exposed, on the concave lateral surface of the branchial basket (fig. 3), a series of three horizontal and five vertical vessels lying in the connective tissues that cover the lateral surface of the basket, these vessels quite certainly being venous and not lymphatic ones, for they can be injected from the brachial vein of T. J. Parker's (1894) descriptions. The vertical vessels overlie the lines between the outer edges of each two adjacent gill-pouches. The horizontal vessels lie one at the dorsal edge of the lateral surface of the branchial basket, one at the ventral edge of that surface, and the third one midway between the other two. When these venous vessels and the

enclosing tissues are removed, it is seen (figs. 4 and 5) that the middle horizontal vessel overlies a line formed by the ventral edges of the dorsal constrictores superficiales, the fibres of those constrictores running antero-

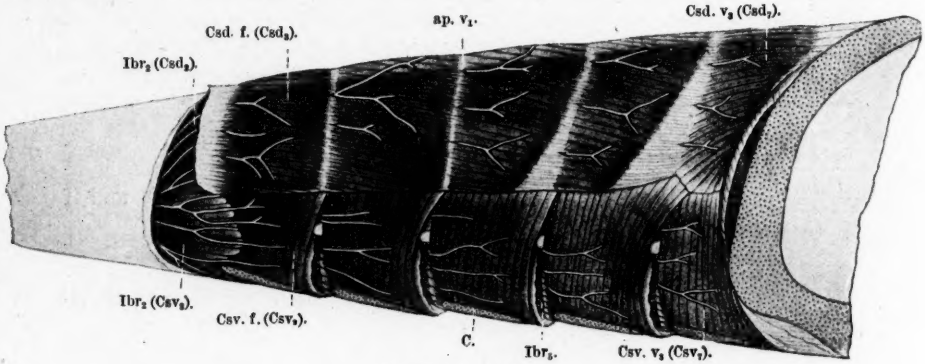

FIG. 4. $\times 1\frac{1}{2}$.

posteriorly and overlapping externally the fibres of the ventral constrictores, which here run ventro-dorsally. Directly internal to the ventral edge of each dorsal constrictor the corresponding ventral constrictor is crossed by

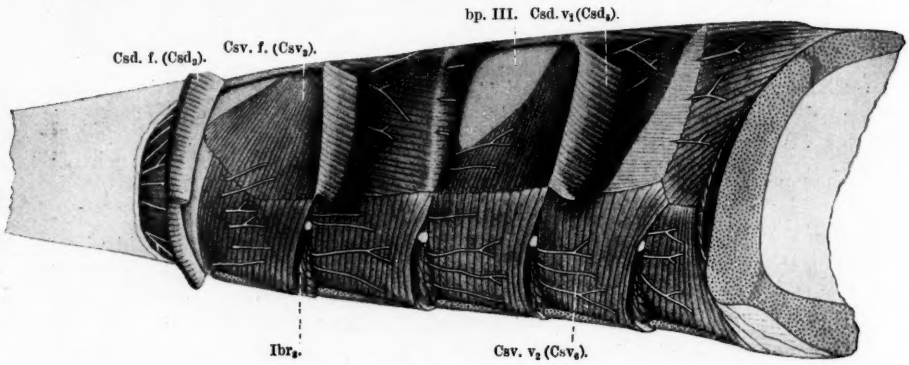

FIG. 5. $\times 1\frac{1}{2}$.

a horizontal aponeurosis, and this aponeurotic line must be the horizontal tendon described by both Tiesing and Marion in these fishes, unless it be that that tendon is simply the ventral edge of the continuous sheet formed by the dorsal constrictores. Tiesing says of this so-called tendon (Sehne)

that it forms the boundary between the dorsal and ventral constrictores. Marion says that it starts anteriorly "from the lateral end of the hyomandibular cartilage and, running along the anterior surface of the gill region, connects with the propterygium and continues back in the lateral region, affording insertion to both the dorsal and ventral constrictores." No such tendon was found in either of my three specimens, and it is evidently represented in the aponeurotic line above referred to, and to be later more particularly described. Marion says that the middle branchial ray in each arch runs outward to this tendon. In my three specimens the outer end of that ray lies at a relatively considerable distance ventral to the aponeurotic line, and there is no tendon related to it.

The dorsal constrictores superficiales, as identified by both Tiesing and Marion, form a continuous muscle-sheet. The ventral constrictores form such a sheet on the ventral surface of the branchial basket, but on the lateral surface of that basket they are separate and distinct muscles. Each of these muscle-sheets is crossed, transversely to the body, by five aponeurotic lines. The dorsal lines start at or near the mesial edge of the sheet and, running laterally in nearly straight lines that diverge slightly anteroposteriorly, reach the lateral edge of the branchial basket and there turn ventrally along its lateral surface. The posterior four lines overlie the lines between each pair of the five gill-pouches, the anterior line lying along the dorso-anterior edge of the anterior pouch. That part of each of these five lines that lies on the dorsal surface of the branchial basket thus overlies the line where the branchial rays of the related arch bend abruptly posteriorly in the outer wall of the next posterior gill-pouch. On the lateral surface of the branchial basket, the posterior four aponeurotic lines all extend ventrally to the ventral edge of the muscle-sheet in each of my three specimens, the anterior line also so extending in both specimens of *Raia clavata*. In the one specimen of *Raia radiata* (fig. 6) this anterior line extended ventrally to the same horizontal level as the posterior lines, but it did not there reach the ventral edge of the muscle-sheet, this apparently being a specific characteristic. In all three specimens the ventrolateral ends of the dorsal aponeuroses of the second and third vagus arches have each become a wide fascia instead of a simple aponeurotic line. In their course along the lateral surface of the branchial basket the several aponeurotic lines have no relations to the branchial rays, those rays not extending downward on to this surface of the basket.

The ventral aponeurotic lines start at or near the mesial edge of the ventral muscle-sheet, and have a lateral and diverging course similar to that of the dorsal lines, but all of them are somewhat curved. When each of the posterior four lines reaches the ventro-mesial edge of the gill-opening

of the next anterior gill-pouch, it curves posteriorly along that edge and then continues onward almost to the anterior edge of the next posterior gill-opening, this part of each aponeurotic line thus having no relation either to the line between two gill-pouches or to the line of the bend in the branchial rays. The anterior line of the series has a strictly similar course, but as there is no gill-pouch anterior to it, it does not cross the ventro-mesial edge of a gill-opening.

Overlying each of these aponeurotic lines, both the dorsal and the ventral ones, there is a vein and an artery, the veins being branches of the dorsal and ventral horizontal veins on the lateral surface of the branchial basket, and the arteries being branches of certain of the branchial arteries.

The muscles related to the glossopharyngeus and first two vagus arches

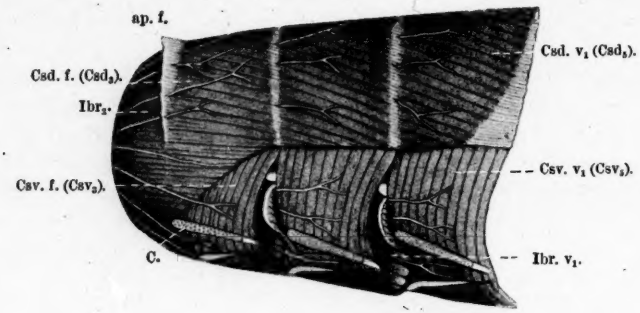

FIG. 6. $\times 1\frac{1}{2}$.

are practically similar, and are, as described by both Tiesing and Marion, the musculi constrictores superficiales, interbranchiales, interarcuales II. (arcuales), and adductores. The constrictores superficiales of these three arches are the muscles Cs_4, Cs_5, and Cs_6 of Tiesing's and Marion's descriptions, and they are assigned respectively, by both those authors, to the first, second, and third vagus arches. The muscles in these three arches being practically similar, it will suffice to describe them in the glossopharyngeus arch alone, and it will be best to begin with the musculus interbranchialis.

The musculus interbranchialis of the glossopharyngeus arch (fig. 9) lies upon the anterior surfaces of the branchial rays of that arch, between those rays and the posterior wall of the first gill-pouch, and it is separated into dorsal and ventral portions in part by the straight middle ray of the arch and in part by the aponeurotic line that lies upon the anterior surface of the proximal portion of that ray. The fibres of the dorsal half of the muscle have their origins on the ray, on the related aponeurotic line, and

on the epibranchial of the arch, and, running dorsally, but spreading both mesially and laterally, they all reach the line of the outer surfaces of the two gill-pouches between which they lie. There they are all, excepting a few lateral bundles, inserted on the dorsal linear aponeurosis related to their arch, that aponeurosis being the second one of the series of five, and the fibres of the interbranchialis being inserted on it throughout its entire length. Ventral to the ventro-lateral end of this aponeurosis, along the line between it and the outer end of the middle branchial ray of the arch, the few remaining bundles of this dorsal portion of the interbranchialis have their insertions in connective tissues of the region.

The fibres of the ventral half of the musculus interbranchialis of this arch have their origins on the middle branchial ray of the arch, on the related aponeurotic line, and on the ceratobranchial of the arch, and they run ventrally, spreading mesially and laterally. A few bundles of the mesial fibres of the muscle, when they reach the level of the ventral surfaces of the two gill-pouches between which they lie, turn, in preserved specimens, sharply laterally for a short distance, and then sharply postero-mesially, and are inserted on the lateral edge of the large median fascia on the ventral surface of the head, immediately internal to the musculus depressor hyomandibularis. The double bend in this muscle in preserved specimens gives to it, in superficial view and as shown in fig. 2, the appearance of arising from the external surface of the ventral linear aponeurosis of the arch; but this appearance is misleading, for the fibres actually lie in the plane of, and mesial to, the other fibres of the muscle. They represent those portions of the proximal fibres of the primitive constrictor of the arch that lie ventral to the triangular piece cut out to form the adductor of the arch, these fibres not having been later subjected to a separation into interbranchialis and constrictor superficialis muscles. They correspond to those fibres of the primitive constrictor that are described by Vetter, in the Selachii, as the deeper fibres of that constrictor, and they were correctly so considered to be by Tiesing. Marion, on the contrary, considers them to be overdeveloped fibres of the interbranchialis (1895, p. 17). Similar muscles are found in the first, second, and third vagus arches, and there are corresponding dorsal muscles in the second and third vagus arches; the ventral muscles apparently being serial homologues of the depressor hyomandibularis, and the dorsal muscles serial homologues of the levator hyomandibularis.

The remaining fibres of the ventral portion of the glossopharyngeus muscle belong definitely to the interbranchialis, and are inserted on the ventral linear aponeurosis of the arch up to the point where that aponeurosis turns posteriorly across the ventral edge of the gill-opening of the first gill-

pouch. Beyond that point the fibres are inserted in connective tissues that lie in part upon the external surface of the anterior (proximal) edge of the ventral constrictor superficialis of the arch, and in part along that edge of that muscle, the line of insertion lying along the line between the first and second gill-pouches, and the conditions here being somewhat complicated, as shown in fig. 6.

In the first, second, and third vagus arches strictly similar conditions are found, the musculus interbranchialis of each of these branchial arches of Raia thus extending between the branchial bar of its arch and the dorsal and ventral linear aponeuroses that overlie the lines where the branchial rays of the arch bend posteriorly in the outer wall of the next posterior gill-pouch. In Mustelus the fibres of the dorsal half of each musculus interbranchialis are, when they reach the outer edge of the next anterior gill-pouch, there in part inserted on the extrabranchial of their own arch and in part inserted on the linear aponeurosis that overlies that extrabranchial (Allis, 1917), that aponeurosis extending dorso-anteriorly across the dorsal end of the next anterior gill-opening. Where there are both dorsal and ventral aponeuroses, as is said by Vetter (1874) to be the case in Acanthias, the conditions are doubtless strictly similar, the musculus interbranchialis of each arch of that fish thus undoubtedly lying, as in Raia, between the branchial bar of its arch and the extrabranchial, or related aponeurosis, of the arch. The interbranchiales of Raia and the Selachii are thus quite certainly strictly homologous muscles, notwithstanding the marked difference in direction of their fibres.

There is, as already stated, no interbranchialis in the fourth vagus arch in any of these fishes, and neither Tiesing nor Marion describes it in the facialis arch. It will, however, later be shown that the so-called musculus Cs_2 of these authors' descriptions is the interbranchialis of the facialis arch and not the constrictor superficialis.

Anterior to the distal (external) end of the ventral half of the interbranchialis of each branchial arch of Raia, in the angle between that muscle and the next anterior ventral constrictor superficialis, there is a small muscle (fig. 9), with one to three muscle bellies, which arises in connection with the linear aponeurosis of the arch, and, running laterally, is inserted on the ventral edge of the gill-opening related to that aponeurosis. These muscles are innervated by branches of the nerves that innervate the interbranchialis against which they lie, those branches, in each arch, passing over the posterior edge of the little muscle to penetrate it on its ventral (external) surface. These little muscles have evidently been specialised to act on the gill-openings.

The dorsal and ventral constrictores superficiales of the glosso-

pharyngeus arch are represented in the muscle fibres that lie upon the external surface of the second gill-pouch, and hence between the second and third dorsal and ventral linear aponeuroses, those aponeuroses being related, respectively, to the first and second gill-openings and also to the bends in the branchial rays of the glossopharyngeus and first vagus arches. The fibres of the dorsal constrictor, the muscle Csd_4 of Tiesing's and Marion's descriptions, all run antero-posteriorly, and, excepting a few ventro-lateral bundles, all extend from one aponeurosis to the other. The few ventro-lateral bundles referred to incline somewhat ventro-posteriorly, and do not reach the first vagus aponeurosis, ending, without evident insertion, along the free ventral edge of the muscle.

The fibres of the ventral constrictor superficialis, the muscle Csv_4 of Tiesing's and Marion's descriptions, run, from in front, postero-mesially, extending between the two related ventral linear aponeuroses. These two aponeuroses are, as already stated, curved, each crossing the ventro-mesial edge of the gill-opening next anterior to it, and then continuing posteriorly toward the middle of the length of the next posterior gill-opening. The fibres of the constrictor, extending between these two aponeuroses, are accordingly inclined, progressively, more and more mesially the nearer they lie to the lateral edge of the branchial basket, and finally acquire a course parallel to and along the anterior edge of the first vagus gill-opening. These lateral, and hence distal, fibres of this portion of the constrictor are directly contiguous with fibres that arise from the antero-lateral edge of that terminal part of the glosso-pharyngeus aponeurosis that lies between the glossopharyngeus and first vagus gill-openings, and these fibres together form a broad band which, running laterally and slightly anteriorly, turns over the ventro-lateral edge of the branchial basket and then upward along its lateral surface until it reaches the ventral edge of the dorsal constrictor of the arch. There the muscle band is crossed by the horizontal aponeurosis, already described, that lies directly beneath the ventral edge of the dorsal constrictor superficialis of the arch. Dorsal to this horizontal aponeurosis, the muscle band continues upward along the lateral surface of the branchial basket and then a short distance mesially along its dorsal surface, but the several bundles of fibres that form the band here become successively shorter, from the anterior to the posterior edge of the muscle, the muscle thus presenting the appearance of a band that has been cut across diagonally. The dorsal ends of most of these bundles have no special insertions, excepting in the connective tissues that cover the underlying first vagus branchial pouch, but the longer, posterior ones are inserted on the internal surface of the dorsal constrictor superficialis

of the arch, in the angle between that constrictor and the interbranchialis of the first vagus arch.

The ventral constrictor superficialis of this fish thus corresponds to the dorsal constrictores of Mustelus (Allis, 1917) in that the proximal fibres of the muscle extend between the linear aponeurosis of their own arch and that of the next posterior arch, while the distal fibres have a ventro-dorsal course between the gill-openings related to those two aponeuroses. Along the line where these ventro-dorsal fibres of the muscle of Raia pass over the ventro-lateral edge of the branchial basket, they are crossed by a little bar of cartilage which lies upon their external surface, loosely attached to them by connective tissues. Mesial to this bar, the gill-opening of the first branchial pouch overlaps externally the anterior (proximal) edge of the ventro-dorsal fibres of the constrictor, and that edge is there also overlapped externally by the outer ends of certain of the fibres of the ventral portion of the interbranchialis of the arch, as already described. Anterior to the anterior end of the little bar of cartilage, and for a short distance dorsal to it, there is, on the external surface of the anterior edge of the constrictor muscle, a line of tough connective tissue which gives insertion to certain fibres of the muscle and also to certain of the fibres of the interbranchialis of the arch, as shown in fig. 6 and as already referred to when describing the musculus interbranchialis. Dorsal to this line of tough connective tissue, the constrictor muscle passes between the outer ends of the middle branchial rays of the glossopharyngeus and first vagus arches, completely filling the space between them. There are five of the little bars of cartilage above referred to, one related to each of the ventral constrictores, and they have already been described by Max Fübringer (1903) in this fish and others of the Batoidei, but he says that they each lie on the outer surface of the related musculus interbranchialis, this being due to a misconception of the homologies of these muscles.

In the first and second vagus arches the constrictores superficiales are strictly similar to those above described in the glossopharyngeus arch. In the third vagus arch the conditions are somewhat different. The dorsal and ventral constrictores superficiales of this arch are the muscles Csd_7 and Csv_7 of Tiesing's and Marion's descriptions, and they are considered by them to belong to the seventh visceral, or fourth vagus, arch. The mesial fibres of both the dorsal and the ventral constrictor separate, as already explained, as the deeper fibres of Vetter's descriptions of the Selachii. The remaining fibres of that part of the dorsal constrictor that lies on the dorsal surface of the branchial basket run posteriorly and somewhat mesially from the linear aponeurosis of

their arch to the hind edge of the fifth gill-pouch. There the lateral fibres of the muscle are inserted by ligamentous tissues on the shoulder girdle, the remaining fibres passing over the hind edge of the pouch and then turning downward along its posterior wall to have their insertions on it, this wall of the pouch lying against the musculus trapezius and inclining strongly ventro-anteriorly. On the lateral surface of the branchial basket the dorsal and larger portion of the fibres of the dorsal constrictor all arise from the dorsal linear aponeurosis of their arch, but the ventral fibres arise from an aponeurotic line that is evidently the homologue of the horizontal aponeuroses of the more anterior arches. This horizontal aponeurosis of the third vagus arch always begins at the point where the horizontal aponeurosis of the second vagus arch meets the dorsal linear aponeurosis of the third vagus arch, and it has a curved, or angular, ventro-posterior course. The ventral fibres of the lateral portion of the dorsal constrictor of the arch always arise from the dorsal edge of this aponeurosis, those fibres of the ventral constrictor that have a ventro-dorsal course being inserted on its ventral edge. The posterior fibres of that part of the ventral constrictor of the second vagus arch that has a ventro-dorsal course are also inserted on this aponeurosis, in each of my three specimens, there overlapping externally the fibres of the third vagus arch. From this surface of origin the fibres of the dorsal constrictor of the third vagus arch run dorso-posteriorly, the ventro-posterior ones inclining more and more dorsally, and they all pass over the hind edge of the fifth gill-pouch and are inserted on the posterior wall of that pouch.

The ventral constrictor of this arch, the muscle Csv_7 of Tiesing's and Marion's descriptions, closely resembles the muscles of the more anterior arches excepting in that its ventro-dorsal fibres end at the horizontal aponeurosis of the arch, above described, and do not there pass upward internal to the dorsal constrictor of the arch. On the ventral surface of the branchial basket, the fibres of this constrictor, running postero-mesially, turn dorso-postero-mesially over the hind edge of the fifth gill-pouch and there separate into four or five parts which all pass between the musculi coraco-branchiales, or between parts of those muscles, and are inserted in part on the posterior wall of the fifth gill-pouch and in part on the membranous wall of the pericardial cavity.

Each musculus interbranchialis is innervated by branches of the nerve of its arch, those branches running outward on the anterior surface of the muscle. Most of these branches, when they reach the outer edge of the muscle, penetrate it, and traversing it and the related linear aponeurosis issue, at the hind edge of the latter aponeurosis, on the dorsal surface of

the next posterior constrictor superficialis. Such branches are found in each arch, going to all portions of the next posterior constrictor superficialis, excepting only the dorso-posterior corner of the ventral constrictor, and they unquestionably innervate these muscles; the constrictor superficialis that lies next posterior to a given aponeurosis thus belonging to the arch to which that aponeurosis is related. The dorso-posterior corner of the ventral constrictor of each arch is apparently innervated by branches of one or two of the large branches related to the next posterior interbranchialis. This branch (or branches), when it reaches the outer edge of the interbranchialis to which it is related, turns anteriorly on to the dorso-posterior edge of the dorso-posterior end of the ventro-dorsal fibres of the constrictor superficialis of the next anterior arch, and sends branches into it, as shown in figs. 7 and 8. In four of eight cases that were examined,

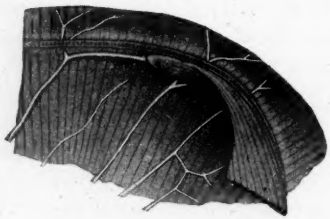

FIG. 7. $\times 1\frac{1}{3}$.

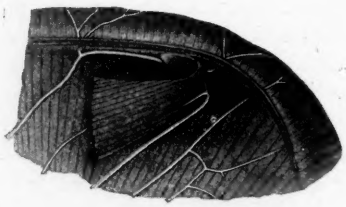

FIG. 8. $\times 1\frac{1}{3}$.

a portion of the fibres so innervated formed a muscle bundle that was somewhat separate from the remainder of the muscle, this suggesting a muscle similar to the one found in corresponding position, and with similar innervation, in the ventral half of the arch, and there differentiated in reference to some action on the gill-opening. This ventral muscle I consider to be derived from some part of the muscle of the arch to which the nerve that innervates it belongs, for there is no apparent reason whatever to assume that it has any other derivation. The corresponding dorsal muscle would then seem to be a similar muscle, but there in process of displacement and disappearance; for I do not believe that the conditions there presented represent a stage in a change of innervation of certain fibres of the constrictor superficialis of a given arch from the nerve of its own arch to that of the next posterior arch. If it be assumed that they do represent a stage in such a change of innervation, then it must be explained why these little muscles are not differentiated in relation to the gill-openings of the fifth branchial pouches as well as to those of the more anterior pouches, for no such muscles, either dorsal or ventral, are found

related to those openings. If, on the contrary, these little muscles are derived from some part of the primitive constrictor of the arch to which the nerve that innervates them belongs, then their absence in relation to the fifth gill-openings is fully explained by the absence of musculi interbranchialis and constrictores superficiales in the fourth vagus arch of either side.

In the third vagus arch the muscles are all innervated exactly as in the more anterior arches, no branch of the nerve of the fourth vagus arch having, so far as could be determined, any relations to any of them.

A musculus adductor branchialis is found in each of the four branchial arches above considered, and also a small musculus interarcualis II. (arcualis), this being as both Tiesing and Marion have stated.

From the above descriptions of the muscles related to the glossopharyngeus and first three vagus arches of Raia, it is evident that the primitive constrictor muscle of each of those arches, when it reached the related dorsal and ventral linear aponeuroses, each turned posteriorly above the next posterior gill-pouch and then extended onward to the linear aponeurosis that lies along the hind edge of that pouch. Whether or no the fibres of the muscle then still continued onward, overlapping the fibres of the next posterior constrictor, cannot be determined from my dissections. Dohrn's (1884) figures of longitudinal vertical sections of embryos of Torpedo, however, strongly favour the assumption that the fibres of each dorsal constrictor were so continued posteriorly; for these constrictores are shown by him as a continuous line of muscle fibres running posteriorly above the three vagus gill-pouches, but partially interrupted between the glossopharyngeus and first vagus pouches. The ventral constrictores are, on the contrary, shown by Dohrn each turning posteriorly above the next posterior gill-pouch, and definitely ending when it reaches the constrictor of the next posterior arch. That the fibres of the ventral constrictores should there definitely end, while the fibres of the dorsal constrictores continue onward beyond the corresponding points, seems to me improbable; but, however it may be, the conditions, as shown by Dohrn, definitely confirm my conclusion that the interbranchialis muscle of each arch was primarily continuous with the constrictor superficialis that overlies the gill-pouch next posterior to it.

The musculi constrictores superficiales of Raia are thus strictly comparable to those in the Selachii, instead of being markedly different from them, as they would be if, as Tiesing and Marion both maintain, the muscle of each arch lay anterior to the gill-opening of the gill-pouch next anterior to that arch. Marion probably here simply accepted Tiesing's earlier and uncontested statement regarding them, and Tiesing evidently

based his conclusion wholly on what he considered to be the innervation of the muscles, without giving any consideration to the resulting impossible position of the ventro-dorsal fibres of each ventral constrictor. According to him, the muscle Cs_3 of his descriptions is innervated by "feinen Seitenästen des N. Glossopharyngeus," and the muscles Cs_4–Cs_7 each, respectively, by corresponding branches of the first to the fourth vagus nerves. No such branches could be found, in any of my specimens, going to the muscles indicated.

The constrictores superficiales of the Batoidei and Selachii thus being homologous, it is practically certain that the linear aponeuroses related to those muscles also are. The aponeuroses in each arch of Raia must then be, as in the Selachii, structures developed, during the life of the individual, as the result of the passage of a primitively continuous muscle over an underlying skeletal structure; and if these underlying structures are not simply the angles formed by the bends in the dorsal and ventral branchial rays, there must have been, primarily, independent extrabranchials in this fish that later fused with the branchial rays to form the flattened and partly fused outer ends of those rays, that are actually found in the adult. But, however this may have been, the underlying structures must have had, in embryonic stages, a greater distal extent, relative to the muscles, than they actually have in the adult, for each of the dorsal aponeuroses extends distally considerably beyond the branchial rays of the related arch. The conditions in Raia can then be explained by assuming a descent from a Selachian such as Acanthias, in which there were both dorsal and ventral linear aponeuroses (Vetter, 1874), each aponeurosis extending posteriorly slightly beyond the related edge of the gill-opening of the gill-pouch next anterior to it, as the dorsal aponeuroses actually do in the adult Mustelus (Allis, 1917). The lateral fin of the Batoidei then gradually developing, with the associated flattening of the head and the gill-pouches, the gill-openings would necessarily be forced from the lateral surface of the head, and they have actually been forced upon its ventral surface. The dorsal and ventral branchial rays have been actually, at the same time, forced on to the dorsal and ventral surfaces, respectively, of the branchial basket. This change in position of the gill-openings and the branchial rays would probably first give rise to conditions such as are actually found in the third vagus arch of Raia, the distal end of the ventral linear aponeurosis being simply forced into a curved course, while the corresponding end of the dorsal aponeurosis was left considerably dorsal to the gill-opening and pulled into a curved course, the hollow of the curve being actually directed dorsally. That part of the constrictor superficialis of the arch that primarily lay between the fourth

and fifth gill-openings and had a dorso-ventral course would retain that course, and would still lie between the two related aponeuroses, but it would lie largely dorsal to the gill-openings. In the more anterior arches those fibres of the dorsal constrictor of each arch that lay proximal to the curved distal end of the dorsal aponeurosis of the arch then apparently sheered ventrally over the more distal fibres, and so gave rise to the conditions actually found in those arches. The horizontal aponeurosis across the ventro-dorsal fibres of each ventral constrictor would then be simply the persisting distal portion of the primitive dorsal aponeurosis of the muscle of the arch.

Thus considered, there would be nothing in the muscles of these four branchial arches of Raia that is not strictly comparable with the muscles in the Selachii, excepting only the little muscles that lie, in the dorsal and ventral halves of each of these arches, in the angle between the outer end of the interbranchialis of the arch and the constrictor superficialis of the next anterior arch. These little muscles have no apparent homologues in the Selachii. That they are the homologues of the little bands of fibres that I described in Scyllium (Allis, 1917) as there being in process of differentiation in relation to the gill-openings, I consider wholly improbable, for in that case they would have lost their primitive innervation by the nerve of their arch and have acquired a secondary innervation by the nerve of the next posterior arch.

The muscles Cs_2 and Cs_3 of Tiesing's and Marion's descriptions now remain to be considered, and these muscles are, respectively, related to the first gill-pouch and the facialis arch as the interbranchiales and constrictores superficiales of the more posterior arches are each related to the corresponding gill-pouch and branchial arch. This position, and also their innervation, shows that they are, respectively, the interbranchialis and constrictor superficialis of the facialis arch, and they are so designated by index letters in my figures. They were considered by Tiesing and Marion to be, respectively, the constrictores superficiales of the facialis and glossopharyngeus arches, and as this identification of them has long been accepted, it will simplify the descriptions to still refer to them by the letters given to them by both those authors.

The posterior edge of the first gill-pouch is nearly transverse in position, but its anterior edge is directed quite strongly antero-laterally, the pouch being considerably wider at its lateral than at its mesial edge, and straddling the space between the glossopharyngeus arch and the epibranchial and ceratobranchial of the facialis arch. The branchial rays related to the latter arch all bend posteriorly, at their outer ends, in the outer wall of the first gill-pouch, the middle ray of the series included, and there is

no space between this middle ray and the next adjacent one on either side, as there is in the more posterior arches. A dorsal linear aponeurosis overlies the bend in the dorsal rays and separates the muscles Csd_2 and Csd_3, this linear aponeurosis being strictly similar to those in the more posterior arches but, in *Raia radiata* (fig. 6), differing from those aponeuroses in that it does not extend ventrally to the ventral edge of the muscle Csd_3. As far as the ventro-lateral end of this aponeurosis of *Raia radiata*, the fibres of the muscle Csd_3 extend between it and the aponeurosis related to the glossopharyngeus arch. Ventral to that point the fibres of

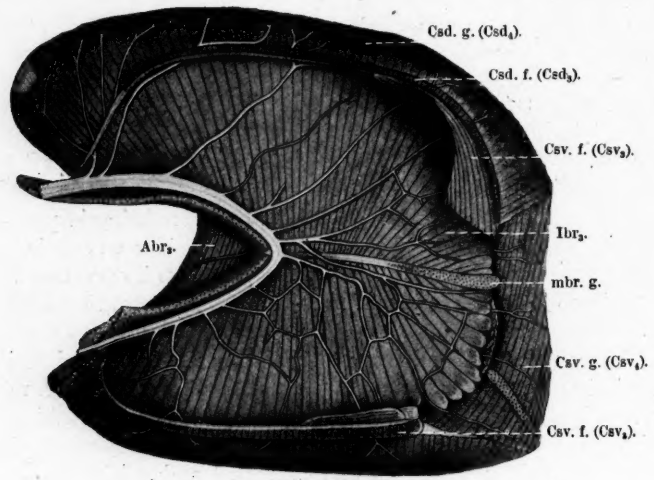

FIG. 9. $\times 1\frac{1}{3}$.

the muscle are directly continuous with those of the muscle Csd_2, and they do not extend posteriorly to the same extent that the dorsal fibres do, simply overlapping the ventro-dorsal fibres of the muscle Csv_3 and there ending, attached by connective tissues to its external surface. The ventral linear aponeurosis overlies, in all these fishes, the bend in the ventral branchial rays of the facialis arch and lies between the muscles Csv_2 and Csv_3, but this aponeurosis is usually less developed than the corresponding ones in the more posterior arches; this being in accord with the position and the less strongly developed condition of the ceratobranchial of the facialis arch. The lateral end of the aponeurosis may even turn toward the glossopharyngeus aponeurosis but vanish before reaching it. Lateral to this lateral end of the ventral aponeurosis, there is a little superficial bar

of cartilage strictly similar to those in the more posterior arches. The distal fibres of the ventral constrictor, Csv_3, run dorsally internal to this little cartilage and then internal to the dorsal constrictor, Csd_3, exactly as in the more posterior arches, but these fibres form a wider and more strongly developed band than in the latter arches. These ventro-dorsal fibres of this constrictor are crossed by a horizontal aponeurosis which is strictly comparable to those in the posterior arches, but it does not, as in those arches, follow the ventral edge of the overlapping portion of the dorsal constrictor, lying, in its anterior portion, dorsal to that edge.

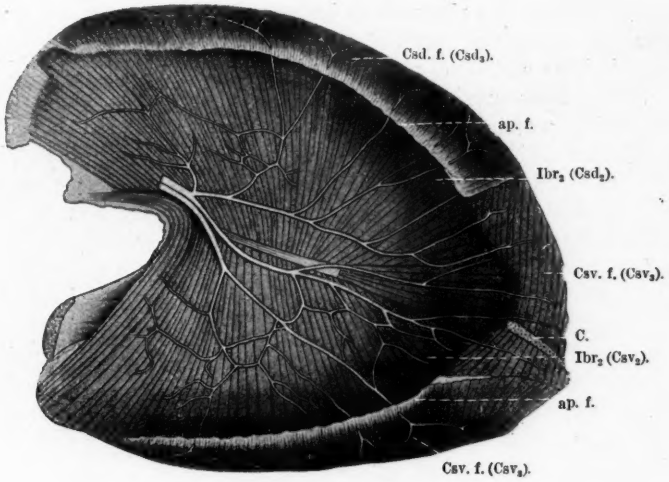

FIG. 10. $\times 1\frac{1}{3}$.

The muscle Cs_2, which is the interbranchialis of the facialis arch, differs in certain important respects from those muscles in the more posterior arches, and is shown, in anterior view, in fig. 10. In this arch the articulating ends of the epibranchial and ceratobranchial are directed laterally, or even antero-laterally, instead of postero-laterally as in the more posterior arches, and because of this no adductor muscle has been cut out of the primitive constrictor of the arch. The fibres that correspond to that adductor have, however, here slipped over on to the anterior surface of those two elements of the branchial bar of the arch, exactly as in the more posterior arches, and certain of the most proximal fibres have acquired insertion on the ventral end of the pharyngeal element of the arch, the so-called hyomandibula, and so given rise to the levator and the depressor

hyomandibularis. The next distal fibres of the primitive constrictor form, in certain specimens, a somewhat separate bundle which passes dorso-ventrally over the lateral edge of the pharyngeal cavity, extending approximately from the level of the dorsal end of the epibranchial to the ventral end of the ceratobranchial, these fibres thus having approximately the position of an adductor of the arch. A few fibres connect this bundle, at the middle of its length, both with the levator and with the depressor hyomandibularis, the conditions varying in different specimens but clearly showing the primitive continuity of these several muscles. The next distal fibres of the primitive constrictor form the musculus interbranchialis, and practically all of them have their insertions on an aponeurosis that overlies the middle one of the branchial rays of the arch—few, if any, of them being inserted either on that ray or on the epibranchial or ceratobranchial of the arch. The aponeurosis does not extend to the outer end of the middle branchial ray, certain of the muscle fibres radiating, fan-shaped, from its outer end, and the dorsal and ventral halves of the interbranchialis there being continuous. Certain of these radiating fibres always pass over the antero-lateral edge of the branchial basket, and they there form, in *Raia radiata*, the ventral portion of the dorsal constrictor Csd_3 of Tiesing's and Marion's descriptions, as shown in fig. 6. Ventral to these fibres, a few bundles of the muscle are inserted, as in the more posterior arches, along the anterior edge of the ventro-dorsal fibres of the ventral constrictor of the arch, the muscle Csv_3 of Tiesing's and Marion's descriptions, all the remaining fibres of the muscle being inserted on the dorsal and ventral aponeuroses that separate this muscle from the muscles Csd_3 and Csv_3 respectively. No musculus arcualis has been differentiated in this arch.

Branches of the nervus facialis go to all parts of the muscles Cs_2 and Cs_3, exactly as in the more posterior arches. There is thus no possible question as to these muscles representing, respectively, the interbranchialis and the constrictor superficialis of the facialis arch.

The m. coraco-mandibularis is an azygous muscle which arises from the membranous ventral wall of the pericardial chamber, and, running forward in the median line, is inserted on the mandibulæ internal to the musculus intermandibularis. It is enclosed in a membranous sheath which arises posteriorly from the shoulder girdle and the ventral wall of the pericardial chamber, and it forms the median ventral fascia of the fish, one layer of the fascia lying external and the other internal to the coraco-mandibularis. The lateral edges of this fascia give origin, on either side, to the musculi depressor mandibularis, depressor hyomandibularis, and depressor rostri, and insertion to the four muscles formed by the deeper proximal fibres

of the constrictores superficiales of the glossopharyngeus and first three vagus arches.

The m. coraco-hyoideus of either side arises largely from the internal surface of the internal one of the two layers of the median ventral fascia above described, but partly also from the ventral (external) surface of the coraco-hyomandibularis, and, running forward between the so-called afferent mandibular artery (arteria thyreo-spiracularis, Dohrn) and the common trunk of the afferent arteries to the hyal and first branchial arches, is inserted on the cartilage called by Gegenbaur (1872) the copula of the facialis arch ("Zungenbein copula"), but by Parker (1876) the hypobranchial of the first branchial arch. This cartilage, which is evidently the hypobranchial of the first branchial arch, was, in one or two specimens that were examined, formed of two pieces, one on either side, the two pieces articulating with each other in the median line.

The m. coraco-hyomandibularis lies internal to the coraco-hyoideus, and arises, posterior to the latter muscle, from the internal surface of the internal one of the two layers of the median ventral fascia, the muscles of opposite sides there being contiguous in the median line. It runs antero-laterally, internal to the common trunk of the afferent arteries to the hyal and first branchial arches, and was inserted, in one of my two specimens, on the hyomandibula alone. In the other specimen it was also so inserted on one side of the head, but on the other side it was inserted by two tendinous ends, one on the hyomandibula and the other on the mandibula. This muscle has, to the afferent arteries, the relations that the coraco-branchialis of the first branchial arch of the Selachii has to those same arteries, and it is apparently the homologue of that muscle.

The mm. coraco-branchiales all arise from the shoulder girdle, partly tendinous and partly fleshy, and separate into three parts. The anterior one of these three parts is inserted by two ends, one on the long anterior end of the fifth hypobranchial of Parker's descriptions (the large posterior copula of Gegenbaur's descriptions), and the other on the third hypobranchial. The next division of the muscle is inserted on the fourth and fifth hypobranchials, and the third division on the fifth ceratobranchial.

The mm. coraco-arcuales communes arise from the shoulder girdle and are inserted mainly on the ventral wall of the pericardial chamber, a small lateral bundle on either side being inserted on the ventral surface of the internal one of the two layers of the median ventral fascia.

The muscle marked × in fig. 1 arises in part from the fascia that covers the dorsal surface of the trunk muscles and in part from the anterior vertebra or vertebræ, and it is inserted, by two tendinous ends, on the ventral surface of the hind end of the chondrocranium, the two tendinous

ends passing one on either side of the nervus vagus. Its innervation was not determined, but it would seem as if it might be a modification of the musculus sub-spinalis of the Selachii.

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EXPLANATION OF FIGURES.

Fig. 1. Dorsal view of the muscles related to the branchial basket on the left-hand side of the head of *Raja radiata*. The m. levator rostri cut and turned back. Sections of the constrictores superficiales dorsales of the glossopharyngeus and first vagus arches also cut and turned back, exposing the underlying gill-pouches and the dorsal ends of the constrictores superficiales ventrales. × 1½.

Fig. 2. Ventral view of the same. M. depressor rostri cut and turned back. × 1½.

Fig. 3. Lateral view of the branchial basket of *Raia clavata*, showing the venous vessels and connective tissues that cover the branchial muscles. × 1½.

Fig. 4. The same, the venous vessels and connective tissues removed, exposing the branchial muscles. × 1½.

Fig. 5. The same, the constrictores superficiales dorsales of the facialis and first

vagus arches cut and turned back, exposing the dorsal portions of the constrictores superficiales ventrales. × 1½.

Fig. 6. Ventro-lateral view of the anterior portion of the branchial basket of *Raia radiata*. × 1½.

Fig. 7. Anterior view of a branchial diaphragm of *Raia clavata*, showing the dorsal end of the constrictor superficialis ventralis of the next anterior arch. × 1⅓.

Fig. 8. The same, the constrictor superficialis ventralis pulled down so as to show the nerve that innervates it. × 1⅓.

Fig. 9. Anterior view of the m. interbranchialis of the glossopharyngeus arch of *Raia clavata*, the dorsal and ventral constrictor superficialis of the arch forced outward so as to be seen in the figure. × 1⅓.

Fig. 10. Similar view of the m. interbranchialis of the facialis arch of *Raia clavata*. × 1⅓.

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Abr_3.	M. adductor branchialis of glossopharyngeus arch.
ap. f.	Linear aponeurosis related to the facialis arch.
ap. g.	,, ,, ,, ,, glossopharyngeus arch.
ap. v_{1-3}.	,, aponeuroses ,, ,, first to the third vagus arches.
bc. I–V.	First to fifth branchial clefts.
bp. I–V.	,, ,, ,, pouches.
C.	Little bars of cartilage related to each m. constrictor superficialis ventralis.
Carc.	M. coraco-arcuales.
Csd. f.–Csd. v_3.	Mm. constrictores superficiales dorsales of the facialis, glossopharyngeus, and first three vagus arches.
Csd_2–Csd_7.	The same, as identified and lettered by Tiesing and Marion.
Cmd.	M. coraco-mandibularis.
Csp_5.	Proximal bundle of fibres of second vagus (fifth visceral) arch.
Csp_6.	,, ,, ,, third vagus (sixth visceral) arch.
Csv. f.–Csv. v_3.	Mm. constrictores superficiales ventrales of the facialis, glossopharyngeus, and first three vagus arches.
Csv_2–Csv_7.	The same, as identified and lettered by Tiesing and Marion.
Dhym.	M. depressor hyomandibularis.
Dmd.	,, ,, mandibularis.
Dr.	,, ,, rostri.
Ibr_2.	,, interbranchialis of facialis arch.
Ibr_3.	,, ,, of glossopharyngeus arch.
mbr. g.	Middle branchial ray of glossopharyngeus arch.
mbr. v_1.	,, ,, ,, of first vagus arch.
Lr.	M. levator rostri.
Tr.	,, trapezius.
×.	M. subspinalis (?).

THE PRIMORDIAL CRANIUM OF PŒCILOPHOCA WEDDELLI (WEDDELL'S SEAL), AT THE 27-MM. C.R. LENGTH.

By Professor EDWARD FAWCETT, M.D. Edin., *University of Bristol.*

(Illustrated by drawings of models.)[1]

THE embryo was kindly supplied to me by Prof. D'Arcy Thompson of St Andrews University; it had been preserved in formalin since 1892, and was in as fair condition as could be expected after such a long stay in formalin. It was embedded in paraffin, and cut into sections of 20 microns in thickness. Its total crown rump length was 27 mm. The sections were experimentally stained, some of them with Delafield's hæmatoxylin and eosin, some with thionin, and others with Mallory's triple connective-tissue stain. Of these stains the last proved to be the most satisfactory, but the result was far behind what one usually gets with this stain, no doubt on account of the long stay in formalin and the want of a mercury fixative. It is my experience that Mallory's stain is not so effective in those cases in which there has been prolonged soaking in formalin, and the chief failure is in regard to the fuchsin part of the stain. The preliminary stain in fuchsin seems to take readily enough, but is only indifferently fixed by the phospho-molybdic acid, so that it tends to wash out after the sections are passed through the anilin-blue. However, the latter does give a really satisfactory stain for the cartilage and a magnificent stain for bone, so, apart from the general somewhat blue appearance of the sections, it is pretty easy to determine what is cartilage and what is what is called procartilage. Neither hæmatoxylin nor thionin gave anything like such good results, and the sections so stained were re-stained in Mallory's stain.

Being a somewhat rare animal, and possessing most of the peculiarities of the seal group, it was considered important that a model should be made of the chondrocranium as a whole, to be supplemented by additional models of certain parts which cannot be studied in any complete model. It was further hoped that perhaps the affinities of the seal to other groups of carnivora might be determined, more particularly as to whether it lay nearer the bear group or the cat group, as the position is by no means clear at the present time; but there are many difficulties.

[1] The expenses of this research were defrayed by a grant from the University of Bristol Colston Society.

In the first place, there is no sufficient description of the chondrocranium of the bear, nor can one replace that by the dog; for although dogs are common enough, they are practically sacred animals, and the removal of dead embryos from the body of a dog killed in the lethal chamber of a dog's home is looked upon as vivisection, and one cannot obtain embryos in this way!! As I have models of the cat's chondrocranium as well as models of that of the ferret, a comparison will be drawn between that of this seal and those just mentioned, and so far as possible with the known facts in regard to the bear and dog.

Owing to its aquatic habits the seal has naturally undergone some modification of structure—and these largely concern the parts in the nasal region. Thus the lacrimal conducting apparatus is awanting, together with the lacrimal bone; there are no sinuses in the cranial bones, although their representatives are well developed in the chondrocranium. The olfactory region of the nasal capsule is of very small size, the organ of Jacobson is absent, and the auditory ossicles are of large size, and as a consequence the muscles which are attached to them are enormous. The thyroid cartilages show a very primitive form at the stage modelled, and it will be shown that the tectum cranii anterius is of special interest. Taken as a whole the chondrocranium is very simple, and might be used as a standard from which one might work forwards or backwards.

Method of Description.—In accordance with the plan adopted in the case of Microtus and Erinaceus, the primordial cranium of this seal will be treated as consisting of a neural and a visceral part, and the bones will then be described separately.

The Neural Chondrocranium.

The neural chondrocranium will be considered as consisting of the following parts, viz.:—

1. A central stem.
2. Appendages to the central stem.
3. Commissures connecting the central stem with the aforesaid appendages.
4. Lateral structures.
5. Lateral commissures.
6. Dorsal structures.

1. The Central Stem.

The central stem is divisible into three parts, which are from behind forwards the pars chordalis, the pars trabecularis, and the pars interorbitonasalis (Pls. 1, 2).

In the stage now described these parts are all fused together, but there is no difficulty in marking their limits, as will be done later.

The central stem (Pls. 1, 2) as a whole stretches from the anterior margin of the foramen magnum to the tip of the nose. It is wide transversely behind, but narrows as traced forwards, until, when it becomes pars inter-orbito-nasalis, it becomes higher than wide.

The *Pars chordalis* forms posteriorly the anterior margin of the foramen magnum, and at the same time part of each of the occipital condyles. Its posterior margin between these condyles is somewhat concave, the concavity being directed backwards. Its anterior margin is narrow transversely, and only separable from the hinder part of the pars trabecularis by the site of emergence of the notochord and by an imaginary line drawn transversely through the anterior margin of the basi-cochlear fissure. The lateral margins of the pars chordalis are divisible into two segments, viz. a longer posterior and a shorter anterior segment. The longer posterior segment is in part bounded by an imaginary antero-posterior line drawn through the inner margin of the *foramen hypoglossi* from condyle to jugular foramen. Along this line the lateral margin is directly continued into the exoccipital cartilage of its side; for a short distance, however, in front of this continuity the posterior segment of the lateral margin is free, and it here forms the medial boundary of the *foramen jugulare*. The anterior end of the posterior segment of the lateral boundary of the pars chordalis is indicated by a laterally projected process, the *chordo-cochlear commissure*, which, running out at the junction of posterior and anterior segments of the lateral border of the pars chordalis, fuses by procartilaginous tissue with the cochlear segment of the pars cochlearis of the auditory capsule. At the anterior margin of the base of this commissure the anterior segment of the lateral border of the pars chordalis commences. This parallel with its fellow forms the medial boundary of the basi-cochlear fissure. The anterior segments of the lateral boundaries are placed much nearer together than the two posterior segments, and on that account the anterior part of the pars chordalis, viz. that part in front of the chordo-cochlear commissures, is narrower than that behind them. The surfaces of the pars chordalis are superior or caval and inferior. The superior surface of that part which lies behind the chordo-cochlear commissures is concave, that part in front of these commissures is flat. The inferior surface is convex posteriorly, as might perhaps be expected from the condition of the superior surface of the corresponding region; whilst the inferior surface of that part in front of the chordo-cochlear commissures is concave from behind forwards, the concavity being bounded by a lateral ridge on each side.

The chorda dorsalis (Pl. 1) has a somewhat interesting relation to the

pars chordalis. As far forwards as the chordo-cochlear commissures it lies on its caval aspect, then for a short distance it sinks under the perichondrium. It again emerges at about the junction of the pars chordalis with the pars trabecularis, on whose posterior surface it is placed as far as the summit of the *crista transversa*. Practically the part which lies under the perichondrium corresponds with that part of the pars chordalis which lies in front of the chordo-cochlear commissure, the part which many authors have described under the name of pars otica.

The Pars trabecularis (Pls. 1, 2).—This is the region associated with the pituitary body. Its boundaries are determined by imaginary lines, both anteriorly and posteriorly. The posterior boundary is determined by an imaginary line drawn transversely through the anterior wall of the basi-cochlear fissures. The notochord too, emerging, as it does, at about the middle of this transverse line, separates in part the pars trabecularis from the pars chordalis (Pls. 1, 2).

The anterior limit is not so easy to determine, but when careful examination is made with the microscope it will be found that the chondrified pars trabecularis can be traced forwards as a somewhat thin projection under that region to be subsequently described as the region of the middle clinoid processes and there to end as cartilage. A transverse line drawn through the hinder roots of the alæ orbitales will sufficiently delimit this part in front (Pls. 1, 2). The lateral margins of the pars trabecularis extend from behind at the anterior wall of the basi-cochlear fissure to the hinder (post-optic) limb of the ala orbitalis. Each lateral margin at once, at its posterior extremity, gives outwards to the cochlear capsule a cartilaginous bar—the *posterior trabeculo-cochlear commissure*. This commissure separates the *basi-cochlear fissure* behind from the *foramen caroticum* in front, and it is of considerable antero-posterior width. From the middle of the lateral margin of the pars trabecularis another bar of cartilage—the *anterior trabeculo-cochlear commissure*—arises, which, passing outwards and backwards in front of the foramen caroticum, completes this foramen by joining with the cochlear capsule some distance lateral to the posterior trabeculo-cochlear commissure. The remainder of the lateral border is free and forms the medial border of the *spheno-parietal fontanelle*, but a broad, thin lamina of fibrous tissue is attached which seems to serve as an attachment for part of some of the ocular muscles.

The surfaces of the pars trabecularis are two in number, viz. a superior or caval and an inferior. The superior or caval surface is concave about its middle to form the pituitary fossa. This fossa is bounded behind by a somewhat conical *crista transversa*, on the middle of whose posterior aspect the chorda dorsalis lies. The fossa is bounded in front by a large

transverse eminence which corresponds, so far as I can see, with the olivary eminence of the human skull, and this eminence at each lateral extremity is prolonged backwards in the form of a conical projection, which apparently is a middle clinoid process. The pituitary fossa is prolonged under the middle of the olivary eminence as a small deep pit. There is no trace of a pharyngeal canal, and both olivary eminence and middle clinoid processes are at this time in a procartilagium condition resting on the upper aspect of the chondrified part of the pars trabecularis. Whether they really belong to the pars trabecularis or are to be regarded as a backwardly thrust part of the pars interorbito-nasalis I must leave an open question, as younger stages are necessary in order to settle the point. For convenience we may at present regard them as belonging to the pars trabecularis, and regard this structure as terminating at the imaginary line above alluded to as drawn transversely through the hinder margin of each post-optic limb of the alæ orbitales. The inferior surface of the pars trabecularis is marked in the median antero-posterior line by a slight keel-like projection, which is continuous anteriorly with a similar projection on the inferior aspect of the interorbital part of the pars interorbito-nasalis.

The Pars interorbito-nasalis (Pls. 1, 2) may, with the reservation above mentioned, be considered as commencing at the imaginary transverse line drawn through the hinder margin of the post-optic limbs of the alæ orbitales. It is at first of considerable width, because it sends outwards on each side a wing-like extension which is the so-called *ala hypochiasmata* (Pl. 2). This ala at this stage is for the most part in a procartilaginous condition, and it is joined on the upper aspect of its lateral terminal part by the already well chondrified post-optic limb of the ala orbitalis. This limb in individual sections presents the appearance of a separately chondrified nucleus, but successive sections modelled show that it is really part of the post-optic limb of the ala orbitalis, and it is from this that the rectus muscles of the eyeball take their origin. In front of the alæ hypochiasmatæ the pars interorbito-nasalis is fused with the posterior branch of the pre-optic limb of the ala orbitalis (Pls. 1, 2), and so completely fused is it at this stage, that it is quite impossible to say where the line of fusion was. Between the two optic limbs of the ala orbitalis lies the foramen opticum (Pls. 1, 2), which is of considerable size, and its antero-median margin is projected outward for some distance to form a muscular process from which the superior oblique muscle of the eyeball arises. Anterior to the posterior branch of the pre-optic limb of the ala orbitalis the lateral margin of the interorbital part of the pars interorbito-nasalis becomes free, and it bounds medially a fissure, the *foramen præchiasmaticum* (Pl. 1) of Macklin, a foramen which in the seal is a fissure inclined obliquely from behind

forwards and inwards until it nearly meets its fellow anteriorly. Macklin's view is that this foramen is formed from the foramen opticum, and in a sense that may be true, but it is certainly more immediately formed here by the development of a bar of cartilage, which, growing forwards from the front margin of the pre-optic limb of the ala orbitalis, reaches and fuses with the hinder part of the nasal septal part of the pars interorbito-nasalis. (In the cat and ferret this bar of cartilage does not reach the septum nasi, but fuses with the dorsal edge of the cupula nasi posterior.) The part of the pars interorbito-nasalis which has just been described is that part usually alluded to as the interorbital septum, but with the addition of the hinder element, to which are appended on each side the alæ orbitales. Its upper surface between the foramina optica is slightly concave from side to side, and was termed by Voit the lamina hypochiasmata, and it is prolonged outwards into the posterio-median part of the foramen opticum as the ala hypochiasmata. It is slightly concave from before backwards. In front of the lamina hypochiasmata the upper surface is of obscure extent laterally, seeing that it is fused with the anterior limb (pre-optic) of the ola orbitalis; but in front of this, where the foramina prechiasmata exist, it is of triangular form, whose apex is forwards. The inferior surface of the interorbital part of the pars interorbito-nasalis is marked by an antero-posterior keel-like ridge, which is continuous posteriorly with the ridge already mentioned on the pars trabecularis, and anteriorly with the median part of the lower edge of the nasal septal part of the pars interorbito-nasalis, to which it is bent at an angle of something like 130°, open below. Intrinsically the interorbital septum is comparatively narrow, as is determined by the outline of its chondrified part, which, somewhat triangular in coronal section behind, changes anteriorly to a pear-shaped outline with large end downwards. The pars nasalis of the pars interorbito-nasalis is the septum nasi, and at the same time that part of the pars interorbito-nasalis which is included within the nasal capsules. Its detailed description may therefore be with advantage deferred until the nasal capsule as a whole is dealt with. No more need be said here than that it may be divided into two parts, viz. a subcerebral and a precerebral part.

2. Structures appended to the Central Stem.

These are from behind forwards:—

(*a*) The exoccipital cartilages;
(*b*) The auditory capsules;
(*c*) The alæ temporales;
(*d*) The alæ orbitales;
(*e*) The lateral parts of the nasal capsule.

(a) *The Exoccipital Cartilages.*

Each of these projects laterally from opposite sides of the hinder part of the lateral border (as defined above) of the pars chordalis of the central stem. Each is developed by direct outgrowth from the central stem, and, as said above, may only be artificially distinguished from that central stem by an imaginary line drawn antero-posteriorly through the medial margin of the hypoglossal canal. Each then starts by two roots, one in front of and the other behind the hypoglossal canal, and the hinder root bears the condyle on its lower and hinder aspect. The two roots blend lateral to the hypoglossal canal and form a common mass, which for a short distance passes directly outwards as the so-called *lamina alaris*. This lamina alaris separates the auditory capsule from the foramen magnum. Its anterior border near its commencement shoots forwards under the infero-medial aspect of the pars canalicularis of the auditory capsule to form a jugular process, which shows a conical, somewhat downwardly directed, projection, the *paracondyloid process*. The jugular process is attached to the pars canalicularis by dense cellular tissue, but there is no cartilaginous union. Its upper surface is grooved by the lower end of the *sinus venosus lateralis*. Lateral to the jugular process the anterior border of the lamina alaris is bevelled from behind downwards and forwards and placed under the infero-medial surface of the pars canalicularis, from which it is separated by a comparatively wide but gradually diminishing interval, the *recessus supra-alaris*. This interval gradually diminishes when traced from cavum cranii to the exterior, and is ultimately reduced to a mere fissure, the *fissura supra-alaris*, or better, the *fissura exoccipito-capsularis*.

The posterior border of the lamina alaris is sharp, and forms a part of the lateral boundary of the foramen magnum.

The upper surface of the lamina alaris is grooved from behind forwards and inwards by the sinus venosus lateralis, but the inferior surface shows a general broad concavity which serves for the attachment of the rectus capitis lateralis muscle. The lamina alaris is succeeded by the terminal part of the exoccipital cartilage, which is directed backwards in a curve whose convexity is outwards and concavity directed inwards to bound laterally the middle third or so of the foramen magnum. It terminates posteriorly opposite a line drawn transversely through a point just behind the middle of the foramen magnum in a pointed extremity.

The outer convex margin of this segment of the exoccipital cartilage is overlapped by the supraoccipital cartilage, and a fissure filled with connective tissue separates the two. It is only near the extreme posterior end of this border that any cartilaginous fusion exists between exoccipital and

supraoccipital cartilages, so that the exoccipital preserves its independence to a remarkable degree at a comparatively late period.

The medial border, as has already been stated, forms part of the lateral boundary of the foramen magnum.

The upper surface of this segment is crossed in its antero-lateral part by the sinus venosus lateralis.

A few words may now be said with regard to the primary foramen magnum.

It is of large size, and bounded completely by cartilage.

In general shape it may be described as that of a lozenge; its general direction is backwards, but its anterior half has a slight downward inclination. Being lozenge shaped, the foramen may be said to possess four angles, viz. an anterior, a posterior, and two lateral. The anterior angle is obtuse, and occupied in its middle by the chorda dorsalis; it corresponds with the incisura anterior, which is so well marked in some other animals. This anterior angle is formed at the expense of the pars chordalis of the central stem. The posterior angle is very obtuse, and formed at the expense of the conjoined supraoccipital cartilages (tectum cranii posterius). The lateral angles are the most pronounced, and are acute; they are formed between the posterior pointed extremity of the exoccipital cartilage and the supraoccipital cartilage of the corresponding side. The boundaries of the foramen are antero-lateral and postero-lateral. Each antero-lateral boundary is formed from before backwards by, first, the pars chordalis and, second, the exoccipital cartilage. The postero-lateral boundary is formed by the supraoccipital cartilage alone.

(b) *The Auditory Capsules* (Pls. 1, 2, 3, 4, 5, 6).

Each auditory capsule is at this stage in a somewhat imperfect condition owing to the youth of the stage examined, but in general features resembles that found generally in mammals.

Each is roughly pyramidal in form, with base outwards on the lateral surface of the chondrocranium, and with apex directed towards the central stem. The long axis of the whole is placed very nearly at right angles with that of the central stem.

Each consists of two main subdivisions, viz. a *pars canalicularis*, the more lateral, and a *pars cochlearis*, the more medial, and the latter (following Voit) is capable of further subdivision into a "vestibular" and a "cochlear" segment.

The pars canalicularis has but slight attachment to neighbouring parts of the chondrocranium, and that to the lateral wall by means of the

lamina parietalis. The cochlear segment of the pars cochlearis, on the other hand, is moored to the central stem by three distinct commissures, two of which connect it with the pars trabecularis, and are the anterior and posterior trabeculo-cochlear commissures, and the third, which it receives from the pars chordalis of the central stem, is the chordo-cochlear commissure.

The *Pars canalicularis* is that part which more especially lodges the semicircular canals. It represents the general basal part of the pyramidal auditory capsule, and appears on the lateral aspect of the chondrocranium.

It may be regarded as having four surfaces, viz. a *lateral* or basal, which is seen on the lateral aspect of the chondrocranium; an *anterior*, which forms the hinder wall of the primary tympanic cavity; a *supero-medial*, which forms a part of the floor of the cavum cranii, and is characterised by the presence of a large hollow in its middle—the *fossa subarcuata posterior interna* (Pl. 5); an *infero-medial*, which is directed downwards and backwards towards the lamina alaris and processus jugularis of the exoccipital cartilage (Pls. 1, 5). These surfaces may be examined in the order above named.

The lateral surface is roughly triangular in form, with base forwards and apex backwards, the latter, the so-called *cupula*, being hidden from external view by the opercular process of the supraoccipital cartilage. This surface has the following borders: an anterior or basal, a superior, and an inferior; the two latter converge posteriorly, and meet at the cupula.

The anterior or basal border (Pls. 3, 4, 6) is almost vertical, and shows from above downwards, first, a slight convexity, which I take to be the early condition of a *tegmen tympani*; below this is a hollow, which, because it lodges the crus breve of the incus cartilage, is the *fossa incudis*; this is succeeded at a somewhat medial plane by a slight projection, which, since it gives attachment to the processus styloideus, is identified as the *crista parotica*. The lower end of the anterior border merges into the anterior end of the inferior border at a rounded angle, which from the muscles it gives attachment to must be regarded as the *processus mastoideus*.

The inferior border (Pls. 3, 4) commences in front at the processus mastoideus, and terminates behind at the cupula. In its anterior half it is almost straight and horizontal, but in its posterior half it rises somewhat rapidly, to terminate at the cupula. It is semicylindrical in form, and corresponds in the interior with the posterior semicircular canal, hence it is named the *prominentia semicircularis posterior*. The medial side of this segment of the inferior border to within a short distance of the

cupula is in relation with the jugular process and lamina alaris of the ex-occipital cartilage from before backwards, but is actually separated from them by the fissura supra-alaris, or fissura exoccipito-capsularis; the hinder part of this segment of the inferior border is overlapped from without by the processus opercularis of the supraoccipital cartilage.

The superior border (Pls. 3, 4) commences in front at the tegmen tympani, and terminates behind at the cupula. It, like the inferior border, may be divided into an anterior and a posterior segment. The former gives attachment in its whole length to the *lamina parietalis*; the latter, which slopes downwards and backwards to the cupula, is free, forms the lower boundary of the supraoccipito-capsular fissure, is semicylindrical, and caused by the anterior semicircular canal. It is therefore the *prominentia semicircularis anterior.*

The *Lateral* surface (Pls. 3, 4), which is enclosed by these boundaries, is on the whole convex, but about its centre shows a shallow depression, which is bounded above and behind by the prominentia semicircularis anterior, below and behind by the prominentia semicircularis posterior, below and in front by a prominence which, rising up from about the junction of the anterior and posterior segments of the lower border, reaches the basal border just lateral to the crista parotica. This prominence is caused by the lateral semicircular canal, and is termed the *prominentia semicircularis lateralis.* The shallow depression enclosed by these prominences may be termed the *fossa subarcuata lateralis.*

The *Anterior* surface of the pars canalicularis (Pl. 6) forms the posterior wall of the primary tympanic cavity. It is narrow from side to side, but deep from above downwards. Its upper part is slightly hollowed to receive the body of the incus cartilage, and is wider than the lower part. The lower part is grooved, more laterally to lodge the facial nerve, and more medially to lodge and give origin to the stapedius muscle, which is of large size. The groove for the stapedius is deeper than that for the facial nerve.

The *Supero-medial* surface of the pars canalicularis (Pls. 1, 5) is of large size, is inclined mainly upwards, but with a slight tilt medialwards and backwards. It is easily recognised by the large central depression, called from being arched over above by the prominentia semicircularis anterior the *fossa subarcuata anterior*, and from its internal position relative to the pars canalicularis, and to distinguish it from the one on the lateral aspect above described, the *fossa subarcuata anterior interna.*

The supero-medial surface is bounded above in front and behind by the prominentia semicircularis anterior, which anteriorly swells out to form a *prominentia utricula-ampullaris anterior.* In this prominence a well-

marked transverse ridge is present, which recalls a similar condition in the cat. This in the cat is the outward prolongation of the commissura facialis, but as no such commissure exists in this specimen at the stage modelled, perhaps the ridge may represent an early stage in its formation (if it ever do be formed). Owing to incompleteness of chondrification, the prominentia utriculo-ampullaris superior is invaded by an angular extension of the meatus auditorius internus, through which the ampulla of the membranous anterior semicircular canal can be seen.

Below and behind, the supero-medial surface of the pars canalicularis is bounded by a well-marked prominence which lodges in its interior the crus commune of the anterior and posterior semicircular canals, and is called the *prominentia cruris communis*. This prominence posteriorly ends at the cupula, and anteriorly swells out medial to and below the fossa subarcuata anterior interna to form a well-marked medial boundary to the said fossa. From the lower basal angle of the meatus auditorius internus a slit-like extension of that vacuity extends into the anterior terminal part of the prominentia cruris communis. This slit-like extension is separated on the right side from a foramen—the *foramen endolymphaticum*, which transmits the *ductus endolymphaticus*—by a small bar of cartilage, but on the left side this bar has not yet chondrified. The ductus endolymphaticus, which emerges from the foramen endolymphaticum, is a long, at first cylindrical, narrow tube, which after emergence runs alongside the prominentia cruris communis, at first lodged in a groove thereon, but soon it loses immediate contact with the cartilage, and comes to be medial to the sinus venosus lateralis, and is continued backwards as a wide sac-like structure which terminates in a narrow-pointed extremity medial to the supraoccipital cartilage. No pressure vacuity exists in the pars canalicularis, which is rather exceptional, and doubtless to be explained by the want of close relationship between the hinder part of the duct and the cartilage.

The *Infero-medial* surface of the pars canalicularis is triangular in form, and is directed downwards and backwards towards the jugular process and lamina alaris of the exoccipital cartilage, from which it is separated by the recessus supra-alaris. The apical region of this surface reaches outwards almost as far as the cupula, its basal region reaches medialwards as far as the foramen jugulare.

It is bounded above by the prominentia cruris communis, below by the prominentia semicircularis posterior. About its middle there is a deep pit, which burrows into the pars canalicularis medial to the lower end of the prominentia semicircularis posterior; this pit is the *fossa subarcuata posterior* (Pl. 5). Basalwards of this fossa the infero-medial surface swells out to form the *prominentia utriculo-ampullaris posterior* (Pl. 5).

The Pars cochlearis (Pls. 1, 2, 5, 6), which is the antero-medial continuation of the auditory capsule, consists as before said of a "vestibular" and a "cochlear" segment.

The "*Vestibular*" segment is that part especially which shows on its caval aspect the *meatus auditorius internus* (Pls. 1, 5), and on its lateral aspect the foramina vestibuli and cochleæ. It is interposed between the pars canalicularis and the cochlear segment of the pars cochlearis. It presents to view four surfaces, of which one is superior, one medial, one inferior, and the remaining one lateral.

The *superior* surface is small, and grooved to form the upper part of the *sulcus facialis* (Pls. 1, 5), on which the germ of the facial nerve rests. Whether it is ever bridged over by a cartilaginous suprafacial commissure I do not know, as no embryo old enough to determine that point is at my disposal.

The *medial* surface (Pls. 1, 5) is almost wholly occupied by the *meatus auditorius internus*, which, no doubt owing to the young stage modelled, is very large, and not divided into what may be presumed to be its subsequent compartments. The opening is triangular in form, and if the base of the triangle be regarded as its outer side, then each basal angle is projected backwards and outwards in the form of a narrow fissure which, in the case of the upper basal angle, leads to the prominentia utriculo-ampullaris anterior, and in the case of the lower basal angle to the prominentia cruris communis, and at the same time transmits the ductus endolymphaticus on the left side. In Plate 5 the relations of the membranous to the meatus auditorius internus are shown, and it will be noticed that the saccule, the commencement and the terminal coil of the cochlear duct, are visible, also that the ductus endolymphaticus leaves the posterior inferior basal angular fissure above mentioned.

The *inferior* surface (Pls. 2, 5) is small, and directed towards the foramen jugulare. It is almost wholly occupied by the conjoined foramina cochleæ and perilymphaticum.

The *lateral* surface (Pl. 6) forms the medial wall of the primitive tympanic cavity, and from above downwards shows first the sulcus facialis next the foramen vestibuli (fenestra ovalis) which is occupied by the foot of the stapes, finally the promontorium caused by the initial part of the basal coil of the cochlea. Above and in front of the foramen vestibuli a flattened area is caused by the very large tensor tympani muscle.

The "*Cochlear*" segment of the pars cochlearis (Pls. 1, 2, 5, 6) is somewhat small in size; this is markedly the case in comparison with that of the cat (Pl. 11), but it is on the whole perhaps relatively larger than

that of the ferret (Pl. 10). It is moored to neighbouring parts in the following way: viz. postero-medially to the central stem by the small chordo-cochlear commissure, to the pars trabecularis by the anterior and posterior trabeculo-cochlear commissures. It is separated from the central stem by the large basi-cochlear fissure, and from the pars trabecularis by the foramen caroticum. Its surfaces may be described as medial or caval, inferior and antero-inferior. The medial surface is roughly triangular in shape, and at the apex is directly continuous with the caval surface of the posterior trabeculo-cochlear commissure. This surface is comparatively flat, in which respect it contrasts markedly with the condition in the cat, in which it bulges into the cavum cranii to come into pretty close relation with that of the opposite side.

The antero-inferior surface is the largest, and is convex in all directions. It is crossed from below upwards in an antero-posterior direction by the internal carotid artery, but possibly on account of the small size of that artery no sulcus caroticus is visible upon it. To the upper part of this surface the anterior trabeculo-cochlear commissure is attached.

The inferior surface is small, and indented by the common foramen cochleæ and foramen perilymphaticum.

A commissura suprafacialis does not exist at this stage, but there seems to be a small spur on the medial side of the sulcus facialis of the vestibular segment of the pars cochlearis which may represent it.

(c) *The Ala temporalis* (Pls. 1, 2).

This, which is developed separately, is of comparatively small size, is thin and flat, and placed in front of the middle of the anterior trabeculo-cochlear commissure, from which it is separated by dense cellular tissue, which in appearance is very much like that intervening between the cartilages and long bones at a joint. The lateral border of the ala temporalis is notched for the downward passage of the mandibular division of the fifth cranial nerve, and by this notch one may divide the ala into an anterior and a posterior segment. On the caval surface of the ala the Gasserian ganglion, the maxillary and ophthalmic divisions of the fifth cranial nerve rest. The inferior surface, which is not quite so flat as the superior, shows signs of a median antero-posterior rounded ridge, which is the representative of the processus pterygoideus of the ordinary ala temporalis. The inferior surface is subtended by a large wedge-shaped mass of connective tissue, from whose apex the pterygoideus internus muscle arises, and from whose infero-lateral surface the lower (sole) head of the pterygoideus externo arises.

(d) *The Ala orbitalis* (Pls. 1, 2, 3, 4).

This structure, which belongs also to the lateral structures, is of large size, and forms a very important constituent in the floor of the cavum cranii. It may be best described as triangular in form, with its apex directed towards the central stem. Its basal angles are placed in the lateral wall of the cavum cranii. The body or main mass forms at once a part of the floor of the cavum cranii and the roof of the orbital cavity. Its anterior border forms the posterior boundary of the orbito-nasal fissure, and also, after fusion with the hinder part of the nasal capsule, forms a projection over the nasal cavity, of which more will be said later.

The posterior border of the ala forms the anterior boundary of the spheno-parietal fontanelle, and near the central stem develops a backwardly directed process which has all the appearance of an anterior clinoid process. The basal border forms part of the brim or rim of the cavum cranii. The angles of the ala, which are an apical, an anterior, and a posterior basal angle, are of importance and interest. The apical angle is curious, inasmuch as it divides primarily into a pre- and a post-optic limb, of which the former again divides into two.

The post-optic limb from the processus clinoideus anterior turns suddenly downwards and inwards towards the ala hypochiasmata of the central stem and fuses with its outer extremity, which at this time consists of procartilage. It is from this narrow, downwardly directed part of the post-optic limb that the eye muscles, save the superior oblique, take origin, and from its advanced state of chondrification as compared with that of the ala hypochiasmata one can easily distinguish the two.

The pre-optic limb forms the anterior wall of the foramen opticum and then divides into two branches, of which the more posterior is fused with the central stem (interorbital part of it), whilst the more anterior is attached to the hinder part of the subcerebral segment of the septum nasi. Between these two branches a long oblique fissure bounded medially by the upper edge of the interorbital septum is found. A somewhat similar fissure is described by Macklin in man under the name *foramen præchiasmaticum*, and he regards it as being a cut-off part of the foramen opticum. From the condition here and that of the ferret (Pl. 10) and cat (Pl. 11) I prefer to think of it as an isolated part of the orbito-nasal fissure, which isolation has been brought about by the fusion of the anterior branch of the pre-optic limb of the ala orbitalis with the nasal capsule, and the further extension of that branch to the septum nasi. That in a simpler condition is seen in the ferret, in which the anterior branch of the pre-optic limb only reaches the cupula nasi, thus separating the orbito-nasal fissure into a median and

a lateral part, but it does not extend so far inwards as the septum nasi. Not only does this anterior branch of the pre-optic limb of the ala orbitalis cut off this fissure, but it at the same time forms a roof for the hinder part of the nasal cavity, a roof which, however, is perhaps but a temporary one.

The anterior basal angle of the ala orbitalis fuses with the frontal prominence of the pars intermedia of the paries nasi to form the *sphenoethmoidal commissure* and so bound the *orbito-nasal fissure* laterally. It is covered on its outer aspect by the frontal bone. The posterior basal angle is fused with the forward extension of the lamina parietalis, forming in this way the *orbito-parietal commissure.* Not far from the middle of the ala orbitalis two foramina are found; a few small blood-vessels pass through one of them, the other does not seem to transmit anything. A similar condition is to be observed in Tatusia; may they be representatives of the reptilian foramen epiopticum?

(e) *The Lateral Wall of the Nasal Capsule.*

This structure may be conveniently left until the nasal region as a whole is described.

3. Commissures connecting the Central Stem with the Appendages (Pls. 1, 2).

These, which are on each side from behind forwards, the chordo-cochlear, the posterior and anterior trabeculo-cochlear commissures, have been sufficiently alluded to already, and do not require further description.

4. Lateral Structures (Pls. 1, 2, 3, 4).

The structures which may be grouped under this heading are:—

1. The supraoccipital cartilages,
2. The laminæ parietales (parietal plates),
3. The alæ orbitales.

1. *The Supraoccipital cartilage* (Pls. 1, 3, 4) is primarily a separate entity, which rapidly assumes a triangular form. The angles are an anterior, an inferior, and a postero-median. The anterior angle is fused with the lamina parietalis, forming what may be called a *commissura supraoccipito-parietalis*, between whose inferior margin and the pars canalicularis of the auditory capsule is the supraoccipito capsular fissure. Its inferior angle forms a processus opercularis, which overlaps on its outer side both the hinder end of the pars canalicularis and the outer edge of the exoccipital cartilage. It is quite independent of the former, and is

only very slightly fused with the apical region of the latter. The postero-median angle projects over the back part of the cavum cranii and fuses with its fellow to form the tectum cranii proterius, a structure which at the same time forms the upper margin of the primary foramen magnum.

2. *The Lamina parietalis* (Pls. 3, 4, 5).—This, otherwise known as the parietal plate, springs from the anterior half of the upper margin of the pars canalicularis of the auditory capsule. Its hinder margin is at first for a short distance free where it forms the anterior margin of the supraoccipito-capsular fissure, but the greater part of this border is blended with the anterior angle of the supraoccipital cartilage to form the supraoccipito-parietal commissure. Anteriorly the lamina parietalis projects forwards as a more or less sagittally directed plate forming the upper border of the spheno-parietal fontanelle, and ends by joining the posterior basal angle of the ala orbitalis to form the orbito-parietal commissure. From the upper margin of the lamina parietalis an angular plate projects, which has attached to it a somewhat narrow coronally directed bar of cartilage, which would seem to be the lower part of a tectum cranii anterius, seeing that at the vertex, and still in the same coronal plane as this, are to be found two coronally placed cartilages of about the same antero-posterior length as the lower bar just mentioned, which must be the upper parts of a tectum cranii anterius. It is possible that these cartilages occupy the neighbourhood of the future bregma, although the state of ossification is not nearly far enough advanced here to enable one to more than surmise that such is the case; whatever their position with reference to the roof of the older cranium may be, their very forward position in this animal is very striking, and is new to me.

3. *The Alæ orbitales.*—These having been already described with the appendages to the central stem need not be alluded to further.

5. The Lateral Commissures (Pls. 1, 3, 4).

These from behind forwards are the *supraoccipito-parietal*, the *orbito-parietal*, and the *spheno-ethmoidal*.

The position and mode of formation of each of these has perhaps been sufficiently indicated already above, and, taken together with the structures which they connect, they form the greater part of what may be termed the "*rim*" of the cranial cavity. This rim is formed as to one-half from before backwards by the anterior margin of the subcerebral vacuity of the roof of the nasal capsule by the upper margin of the frontal prominence of the pars intermedia of the nasal capsule, by the spheno-ethmoidal commissure, the upper edges of the ala orbitalis, the orbito-parietal commissure,

the lamina parietalis, the supraoccipito-parietal commissure, the upper edge of the supraoccipital cartilage, and, finally, the upper edge of the corresponding half of the supraoccipital cartilage. By the *ensemble* of these, what I have termed the "rim" of the cavum cranii is formed.

6. Dorsal Structures.

These are the structures which lie dorsal to the cavum cranii, and may be termed tectum cranii anterius and tectum cranii posterius.

The *Tectum cranii anterius* (Pls. 3, 4) seems to be composed of four cartilages, two of which lie laterally and project up from that part of the "rim" of the cavum cranii which is composed of lamina parietalis and orbito-parietal commissure. Each lateral segment is only here and there attached to the lamina parietalis by continuous cartilage; for the most part it is separated therefrom by fissures filled with connective tissue, and probably has an independent origin. The remaining cartilages which enter into the composition of the tectum cranii anterius are two, placed one on each side of the middle line in the same coronal plane as those just described, and showing slight signs of fusion with one another. Each is of irregularly quadrilateral form, and its long axis is directed coronally. What the ultimate fate of this tectum is I do not know, nor do I know if the several parts of which it is composed remain separate or fuse together. Its far forward position, situated as it is anteriorly to the coronal plane of the fossa hypophyseos, is very striking.

The *Tectum cranii posterius* (Pls. 1, 3, 4) is situated at the back of the cavum cranii, and forms by its lower margin the dorsal edge of the primary foramen magnum. It is formed by the union of the prolonged postero-median angles of the supraoccipital cartilages.

The Nasal Capsule.

The nasal capsule consists of a septum and lateral parts appended to it. Like that of the other carnivora which I have modelled, viz. the cat and ferret, it is comparatively short and squat, approaching more nearly the human type than that of other quadruped animals, but it consists essentially of the same divisions.

The *septum nasi* (Pls. 2, 7), which is the forward continuation of the central stem, consists of two parts, viz. a subcerebral and a precerebral. The antero-posterior length of the former is about one-third that of the latter. Its height at its commencement behind is very little, but it rapidly increases in height when traced forwards, until at its anterior end this part of the septum is the highest of all. As the lower border of this segment

remains practically constant in level, it follows that the increase in height is due to a gradual rising of the upper border, and this rise is culminated at the crista galli, which means the anterior limit of the upper border of the subcerebral part of the nasal septum. The lower border of the subcerebral part of the septum is wider than the upper border. It is convex from side to side, and thicker behind than in front; the median part of its general convexity is continuous with the keel-like ridge on the under aspect of the interorbital part of the interorbito-nasal septum, and that in turn with the similar ridge on the under surface of the pars trabecularis. This part of the under border is bent at an angle of about 130 degrees with that part of the central stem which lies posterior to it. The upper margin of the subcerebral segment of the nasal septum is thinner than the lower one, and, as before said relative to the lower border, rises from it as it is traced forwards to the crista galli. Actually the plane of this upper border is in continuity with that of the remainder of the caval surface of the central stem behind it; it therefore forms an angle with the lower border, and this angle amounts to about 70 degrees. To the hinder part of this subcerebral segment of the upper border the anterior secondary branch of the pre-optic limb of the apical angle of the ala orbitalis is attached.

The precerebral part of the septum nasi is at its hinder end almost of the same height as the subcerebral segment, but its upper border somewhat suddenly descends for a short distance, after which it runs forwards practically parallel with the lower border. The upper border of this segment gives off on each side that part of the capsule which forms the roof of the corresponding nasal passage, and as the roof arches outwards it follows that the upper margin of this segment of the septum is placed at the floor of a sulcus dorsalis nasi, which extends almost from the front of the crista galli to the tip of the nose. The lower margin runs forwards, continuing the direction of the lower border of the subcerebral part of the septum and maintaining the thickness of the latter. Opposite its middle third is placed on each side an *anterior paraseptal cartilage*, which is separated from the septum itself by a *septo-paraseptal fissure*; anteriorly, however, this paraseptal cartilage, which will be described more fully later, is continuous by its antero-superior limb with that lateral offshoot of the inferior border of the septum called the processus lateralis ventralis. The anterior third of the lower border of the precerebral segment appears to bifurcate into two laterally running laminæ (each of which is a *processus lateralis ventralis*) almost until its most anterior limit is reached, when it becomes single and undivided, projecting suddenly downwards before its termination in the form of a peg-like process. There is no internarial

foramen in the septum, nor is there any organ of Jacobson in which the Phocidæ agree with the Cetacea.

The *Lateral* part of the capsule (Pls. 3, 4, 8) consists of a roof, lateral wall, and a floor. Of these the last is very incomplete.

The *Roof* is narrow from side to side, and is attached medially to the upper margin of the precerebral part of the septum nasi, and it is to be clearly understood that what is now being described is the roof of the precerebral part of the nasal capsule, in other words, the tectum nasi anterius, for there is at this time no intrinsic cartilaginous roof to the subcerebral part. The roof of one narial passage is separated from that of the other by a sulcus dorsalis nasi, whilst laterally it almost insensibly continues over into the lateral wall; not far from its anterior end it is perforated by a small *foramen dorsale*. The anterior end forms the upper margin of the fenestra narina, and there is developed at its outer end a small *processus cupularis*. Postero-laterally the roof is separated from the remainder of the lateral part of the nasal capsule by the *sulcus antero-lateralis*, at whose upper end a large foramen epiphaniale is developed for transmission of the lateral branch of the nasal nerve.

The *Lateral wall* of the nasal capsule as seen from the outside (Pls. 3, 4, 8) is divisible into three parts, viz. a pars anterior, a pars intermedia, and a pars posterior. The *pars anterior* is comparatively short, being about the equal in antero-posterior length of the pars intermedia and the pars posterior taken together. It is deeper behind than in front, has an upper rounded border by which it is continuous with the roof, an inferior border which is free in its whole length, and an anterior border which is short and lies almost at right angles to the upper and lower borders. Posteriorly the pars anterior diverges somewhat from the middle line before merging with the pars intermedia at the sulcus antero-lateralis. The inferior border commences anteriorly at the angle of junction with the anterior border, which angle projects very slightly downwards to form a *processus alaris superior*; behind this, at a short distance, a slight notch is seen, which perhaps may be regarded as an *incisura pre-transversalis*, behind which a downward projection, which is probably the outer end of an incomplete lamina transversalis anterior, is found; this is succeeded by a slight *incisura pro-transversalis*. The remainder of the inferior border is practically straight, and is the maxillo-turbinal. The whole of the lateral wall of the pars anterior is lower in height than the septum, hence that structure is exposed to view when the nasal sac is removed; if that be left in position, then its lateral wall is visible below the lower border of the pars anterior (Pl. 8).

The *pars intermedia* is of large size, lateral projection, and depth, is

easily separable from the pars anterior by the sulcus antero-lateralis, but its separation at first sight is not so obvious from the pars posterior, because the sulcus lateralis posterior is placed so high up and runs a course almost parallel with the outer margin of the subcerebral vacuity of the nasal capsule.

The sulcus antero-lateralis is easily found, its commencement above being sufficiently indicated by the large *foramen epiphaniale*, below which it extends downwards under cover of a projecting hood of cartilage as a deep groove; below this it broadens out into a broad triangular hollow, whose deepest part reaches the inferior margin of the lateral wall of the nasal capsule. The sulcus *postero-lateralis* commences above and in front at the root of the spheno-ethmoidal commissure, and passes backwards parallel with the outer margin of the subcerebral vacuity and only a short distance below it. Each of these sulci has a corresponding ridge on the medial aspect of the lateral wall; thus the upper deep part of the sulcus antero-lateralis corresponds precisely with the crista semicircularis, whilst the sulcus postero-lateralis corresponds with the anterior root of the first ethmo-turbinal and with a ridge common to the spring of the second ethmo-turbinal and the lamina transversalis posterior.

The *Pars intermedia* which lies between these sulci is deep, prominent, and large, wider from before backwards below than above. It may be divided into an upper prominence and a lower one. The upper prominence is the *prominentia frontalis*, so called because it is covered by the frontal bone (Pl. 4). It projects forwards as a sort of hood over the foramen epiphaniale and the deep upper part of the sulcus antero-lateralis. Posteriorly it is connected by the spheno-ethmoidal commissure with the anterior basal angle of the ala orbitalis, inferiorly it is separated by a slight sulcus from the *prominentia maxillaris*. The reverse side of the prominentia frontalis is the recessus frontalis. The prominentia maxillaris is of very large size, and divisible into two surfaces, viz. an anterior and a posterior, of which the latter forms the medial wall of the orbit as the planum antorbitale; at the lower part of the ridge separating these surfaces, the inferior oblique muscle of the eyeball takes origin. The inferior margin of the pars intermedia, in its anterior half at least, forms the hinder part of the maxillo-turbinal. The prominentia maxillaris of the exterior corresponds with the recessus maxillaris of the interior.

The *Pars posterior* (Pls. 2, 8) is, as appears to be common to the seal tribe, of very small size. It is certainly long from before backwards, but narrow from above downwards. It is marked off from the pars intermedia below and in front of it by the sulcus lateralis posterior, and it ends posteriorly at the cupula nasi posterior, which is fused

with the under aspect of the anterior branch of the pre-optic limb of the ala orbitalis.

When the nasal capsule as a whole is viewed from above it is seen to consist of two very distinct parts, which are a subcerebral posterior part and a precerebral anterior part. The subcerebral part is divided mesially by the upper edge of the septum nasi, and embraces the interior of the pars posterior as well as the recessus frontalis of the pars intermedia. There is no tectum to this part save that formed by the anterior branch of the pre-optic limb of the ala orbitalis, as the lamina cribrosa has as yet not developed.

The plane of the upper aspect of the subcerebral part of the nasal capsule is practically that of the rest of the floor of the cavum cranii. Its great width as compared with the greater part of the precerebral segment is very striking; moreover, its antero-posterior length too in comparison with that of the latter is at once noticeable. The precerebral part is wide behind, but narrow in front. It is inclined downwards at a considerable angle with the subcerebral part. This angle or downward inclination is at first somewhat sudden, but later much less. A median dorsal nasal sulcus runs from the front almost the whole length of the dorsal aspect of the precerebral part of the nasal capsule, and at the bottom of this sulcus lies the septum nasi. Towards the anterior part of the precerebral segment one notices on each side of the middle line, and at a little distance lateral to it, the *foramen dorsale.*

The Solum nasi (Pl. 2).—This is very imperfect, but extremely interesting, because it, at this stage at any rate, seems to show a condition closely approximating to that of man. The lamina tranversalis posterior fails to reach the immediate neighbourhood of the septum. There are no posterior paraseptal cartilages. These, however, may possibly develop at a later stage.

The *lamina transversalis anterior* is wanting in its middle segment, being present laterally and medially only. Laterally it exists in the form of a downward projection from the lower margin of the lateral wall of the nasal capsule, as has already been mentioned. Medially it forms that part of the processus lateralis ventralis which lies immediately in front of the anterior paraseptal cartilage. On account of the absence of the middle part of the lamina transversalis anterior the fenestra narina is continuous with the fenestra basalis as in man, a *rostro-ventral fissure* being formed.

The anterior paraseptal cartilage is moderately well developed, but consists of a single lamella only as in man, because there is no organ of Jacobson to be lodged in and supported by it. In man the organ of Jacobson, as is well known, lies against the septum nasi at some distance

above the level of the anterior paraseptal cartilage. In its whole length the anterior paraseptal cartilage is separated from the inferior border of the septum nasi by a septo-paraseptal fissure (Pls. 1, 2, 7). Cartilage and fissure lie opposite the middle third of the lower border of the septum. Anteriorly the cartilage is deepest, and it here divides into two somewhat rod-like branches. The upper of these two branches is fused with the hinder end of the processus lateralis ventralis; the lower branch projects freely forward below and almost parallel with the upper, and is apparently the cartilage of the naso-palatine duct.

The *processus lateralis ventralis* passes laterally from the lower part of the anterior third of the septum nasi, and in coronal section has the appearance of being the result of bifurcation of the septum. For the most part it represents the medial segment of the lamina transversalis anterior.

The Medial Aspect of the Lateral Wall of the Nasal Capsule (Pl. 9).

This is of especial interest on account of the peculiarities which it presents, which seem to be characteristic of the group to which the seal belongs. It is divisible into the same three parts as the lateral aspect of this wall, viz. from before backwards, pars anterior, pars intermedia, and pars posterior. Of these parts the pars anterior is intermediate in size, the pars posterior the smallest.

The *Pars anterior* is concave from above downwards, narrow anteriorly at the fenestra narina, but very deep posteriorly where it is confluent with the pars intermedia, from which it is separated in its upper half by the crista semicircularis, and below that only imperfectly separated by a slight ridge corresponding with the lower part of the sulcus antero-lateralis.

Its lower margin is only slightly inclined towards the septum nasi, but the mucous membrane covering it is prolonged for a considerable distance towards the septum, and forms the soft part of the maxillo-turbinal. A lateral nasal gland and duct—the gland at this stage very small—lie in the lateral wall some little distance above the maxillo-turbinal. No trace of a cartilaginous naso-turbinal can be observed. The pars intermedia is very deep from above downwards, and much wider below than above. It is divided into two parts by the union of the crista semicircularis with the anterior root of the first primary ethmo-turbinal. The part above this root is the *recessus frontalis*, which is of comparatively small size but of considerable depth, so deep anteriorly, that it causes the prominentia frontalis to bulge considerably over the foramen epiphaniale. The deepest part of the floor of the recessus frontalis is perforated for the exit of the

lateral branch of the nasal nerve, which appears on the external surface of the nasal capsule. The perforation is the *foramen epiphaniale.*

Below the connection of the anterior root of the first primary ethmo-turbinal with the crista semicircularis is found that large recess which is the *recessus maxillaris.* This recess, which is at its upper and anterior part partly occupied by the lateral nasal gland, is bounded above and behind from before backwards by the first ethmo-turbinal and by the lamina transversalis posterior. Externally these structures are indicated by a sulcus, which is the sulcus postero-lateralis, which commences above just to the outer side of the anterior end of the spheno-ethmoidal commissure and terminates after an obliquely downward and backward course below the cupula posterior. Its course is nearly parallel with that of the upper margin of the pars posterior. I do not make out any real recessus anterior.

The *Pars posterior* is of very curious form, and characterised by containing the ethmo-turbinals, of which there are two. Its floor is not so complete as usual, since the lamina transversalis posterior at this stage is not sufficiently chondrified to come into close relation with the septum nasi. Its anterior boundary is formed by the anterior margin of the first primary ethmo-turbinal, and its upper wall is the same as the lateral border of the subcerebral vacuity in the nasal capsule above. The concavity of this region is a long narrow one, commencing at the anterior border of the first primary ethmo-turbinal and ending posteriorly at the cupula. It is interrupted about its middle by the second primary ethmo-turbinal, which, lying parallel with the first primary ethmo-turbinal, is in the main attached to the upper surface of the lamina transversalis posterior. It is only when careful stock is taken of the pars posterior that one is able to understand how the lamina transversalis and cupula posterior have been formed by the backward thrust of the nasal sac. The conditions presented to view, not only in the model but in the microscopic sections from which this model was made, are strikinglylike those found in *Dasyurus viverrinus* at the 7-mm. and 9·5-mm. c.r. stages, the only real difference consisting in the direct continuation of the hinder wall of the nasal capsule with the septum in Dasyurus.

Both primary ethmo-turbinals are at this stage of simple form, and the first, which is the largest, shows no sign of bifurcation at its free extremity.

The Visceral Skeleton (Pls. 1, 2, 3, 4).

This consists of the usual parts, and presents little of interest.

The cartilage of the first arch (Meckel's cartilage) ends posteriorly as usual in the malleus cartilage, whose appearance is of the usual kind.

Meckel's cartilage itself passes at first downwards and forwards, and soon comes to be covered laterally by the mandibula; at about the junction of the middle third with the anterior third of that bone it turns suddenly upwards, and becoming narrow blends with its fellow medial and slightly anterior to the bony mandible. At this stage it shows no sign of ossification.

As regards the *Malleus*, all that may be added is that it has inserted in the usual place an unusually large tensor tympani muscle, under whose tendon the chorda tympani nerve runs forwards.

The *Incus* cartilage seems to be somewhat large in proportion to the malleus, and it projects on that account more laterally than usual. Its body bears the usual facet for the malleus, and seems to give off four processes, one which passes forwards along the outer side of the head of the malleus for a short distance, another which passes backwards behind and somewhat medial to the head of the malleus. These two processes taken together may be regarded as affording an unusual amount of articular surface to the head of the malleus. The remaining processes are the crus longum, which descends behind and parallel with the manubrium mallei, and terminates where the latter makes its final bend inwards. It is thus about one-third shorter than the manubrium mallei; the angle between the lower end of the crus longum and the manubrium mallei is occupied by the chorda tympani nerve. The crus breve is very thick, and directed downwards and outwards. It terminates near the upper end of the very small crista parotica in a sharp point. On the lateral side of its root lies the extremely small and just ossifying squamosum.[1]

The Cartilages of the second arch (Pls. 2, 3, 4) are represented by the stapes, the processus styloideus, and the cerato-hyal. The *Stapes* cartilage (Pl. 6), which is perforated by an extremely small atrophied stapedial artery, is connected at its head by dense connective tissue with the medial side of the crus longum of the incus cartilage. Its foot-piece is loosely fitted into the foramen vestibuli of the vestibular segment of the pars cochlearis. There is no trace of any connection between the stapes and the remainder of the hyoid arch.

The processus styloideus is attached by dense connective tissue at its proximal end to the lower part of the crista parotica of the pars canalicularis of the auditory capsule. It soon increases enormously in size, but soon again, after being crossed by the facial nerve on its infero-lateral

[1] According to Weber, *Die Säugetiere*, 1904, pp. 544 and 545, "Wie bei diesen (Cetaceen), werden auch die Gehörknöchelchen massig und schwer."

This statement certainly agrees with what I find here so far as concerns the incus cartilage, but I do not note anything extraordinary about the size of the malleus and stapes cartilages. However, the general statement made by Weber may be correct, and will perhaps account for the large size of the tensor tympani and stapedius muscles.

aspect, becomes narrow and cylindrical, when it is crossed on its dorsal aspect from without inwards by the chorda tympani nerve. It retains a cylindrical form for some distance, and in coronal section is quite circular. Below the level of the lower end of the manubrium mallei it gives origin to the musculus stylo-pharyngeus from its inner side, and during this time its shape in coronal section is transversely oval owing to the fact that the cartilage has at this point turned sharply inwards. On arriving near the back lateral wall of the buccal cavity an interruption in the cartilage takes place, and the succeeding cartilage rapidly assumes a greater calibre, soon itself breaking up into two, of which the more distal bends downwards as the cerato-hyal to articulate with the anterior end of the thyro-hyal and the supero-lateral end of the basibranchial. For a considerable part of its length the processus styloideus lies in close association with the posterior belly of the digastric muscle, being on its dorsal aspect, but at this stage neither the stylo-glossus nor the stylo-hyoid muscle has any direct attachment to it. A well-named cerato-branchial muscle connected not only the cerato-hyal but the segment proximal to it with the thyro-hyal or first branchial cartilage.

The Cartilage of the first branchial arch, viz. the thyro-hyal, is dorsally directly continuous with the superior cornu of the corresponding ala of the thyroid cartilage, and in front of this union the internal laryngeal nerve (which possesses here a ganglion, like that pointed out by Nicholas in man) enters the larynx. The anterior end of the thyro-hyal is connected with the inferior aspect of the outer end of the basibranchial (corpus hyale) by dense connective tissue.

The basibranchial cartilage or corpus hyale is a large transversely disposed cartilage, whose lateral extremities are connected by dense connective tissue with the cerato-hyal above and the thyro-hyal below. Above and below it may be seen the remnants of the thyro-glossal duct; the upper segment consisted of little more than débris of its original structure, the lower one apparently being in complete development.

The Cartilage of the second branchial arch (4th visceral) forms the thyroid cartilage. It is deep posteriorly, the deepness being accentuated by the upper and lower cornua, which are directly continuous respectively with the thyro-hyal and the cricoid cartilage. In the former case the continuity is cartilaginous, in the latter by dense cellular tissue. When traced forward the ala of this cartilage very considerably diminishes in height, until it is no higher or deeper than the thyro-hyal. Having reached the plane of the lateral end of the basibranchial (corpus hyale) it suddenly increases in depth, mainly at the expense of its upper border, which rises up to form a considerable projection, which almost reaches the hinder

margin of the basibranchial. The anterior border of the ala of one side is not fused with that of the other; a comparatively wide interval in fact separates the two. The whole appearance of the ala at this time very strongly resembles that of Tatusia at the 12-mm. stage. Whether a foramen will appear in it at a later period in the same way as it does in the older stages of Tatusia I do not know. The condition is interesting.

The Cartilages of the third branchial arch, viz. the cricoid and arytenoids, are moderately well developed. The former is practically complete, and articulates by dense cellular tissue with the inferior cornua of the thyroid cartilage. The arytenoids are only moderately chondrified, and connected basally by dense connective tissue with the cricoid at the usual place.

The Osseous Skeleton (Pl. 4).

This at the stage modelled consists entirely of membrane or "covering" bones, which are the frontale, parietale, incisivum, maxillare, zygomaticum (malar), squamosum, mandibula, and pterygoid.

The *Os frontale* is in a more advanced state of ossification than the os parietale. It lies lateral to the basal part of the ala orbitalis, the spheno-ethmoidal commissure, and the prominentia frontalis of the pars intermedia of the nasal capsule. It projects for some distance above these cartilages, and is deepest at its middle, tapering off to a point anteriorly, where it overlies the prominentia frontalis.

The *Os parietale* is smaller in size than the os frontale, and is only ossified to a very small extent, forming a quite thin lamella lateral to the lamina parietalis where that is bending forwards over the spheno-parietal fontanelle. It at this stage scarcely projects above the level of the lamina parietalis.

The *Os incisivum* is very small, consisting of a transversely laid plate which closed below that part of the rostro-ventral fissure in the floor of the nasal capsule, which has lost the lamina transversalis anterior. It reaches the processus lateralis ventralis of the solum nasi, but does not send backwards along the medial side of the anterior paraseptal cartilage any paraseptal process; perhaps the stage is too early for this to be ossified.

The *Os maxillare* is of comparatively large size, but very primitive in form at this stage. It consists of a body from which there projects upwards in front of the prominentia maxillaris of the pars intermedia of the nasal capsule a massive ascending or frontal process. This body vertically below the frontal process bifurcates into a lateral vertical and an approximately horizontal lamella. The lateral lamella is the outer

alveolar wall, the median one is the palatine process, which projects but a short distance under the rostro-ventral fissure of the solum nasi towards the septum nasi. From the postero-inferior angle of the body of the maxilla an outward projection arises, which is grooved above by the very large infraorbital nerve, and which lateral to this groove sends upwards a short ascending process; beyond this infraorbital sulcus the maxilla terminates in a sharply pointed zygomatic process, which articulates for a considerable distance with the zygomaticum (malar).

The *Os zygomaticum* is a small rod-like bone, which lies along the lateral aspect of the zygomatic process of the maxillare and projects somewhat beyond it. It is separated by a long interval from the squamosum.

The *Os squamosum* is just in the very beginning of ossification, and forms a small scale of bone on the lateral aspect of the body of the incus cartilage. This is its usual position at the commencement of ossification.

The *Os palatinum* is well formed, somewhat triangular in appearance when seen from the outer side at this stage, with apex upwards. Its basal border is slightly inrolled to form the commencement of its palatine process. The antero-posterior length of the bone slightly exceeds its height.

The *Os pterygoideum* is found almost immediately behind the palatinum, is of some size, and more or less perched on the upper lateral aspect of the cartilaginous humulus, which is of great size.

The *Mandibula* is of large size, and stretches from within a short distance of the malleus cartilage behind to the anterior end of Meckel's cartilage, whose general course it very closely follows. The condyle is unossified, but there is a small ossified processus coronoideus. Near its anterior end, that is, at the junction of the hinder two-thirds with the anterior third, the bone takes a sudden bend upwards, just as Meckel's cartilage does, and in the concavity of the bend an incisure is developed to allow the outward passage of the nervus mentalis. From the medial side of this part there arises an internal alveolar wall, which arches upwards over the outer side of Meckel's cartilage. At this stage no accessory cartilages are formed anywhere in connection with the mandibula.

General Conclusions.

One of the most striking facts about the primordial cranium of Weddell's seal at the stage above described is its extreme simplicity, and, with the exception of a somewhat specialised nasal capsule, it might very well serve as a standard from which to work backwards or forwards in phylogeny. The great preponderance of the cerebral segment over the nasal region is

very noticeable, and its almost circular appearance as viewed from above gives it an almost human appearance.

The connections which the chordal part of the central stem form with the cochlear capsule (one on each side) are simple in the extreme, and really are outgrowths of the chordal plate itself. Then too the trabeculo-cochlear commissures are of a very simple type. The central connections, however, of the ala orbitalis with the central stem are essentially, so far as I know, signs of a comparatively high stage of evolution. They appear first in carnivora, and are repeated in man. That the post-optic limb connects through the ala hypochiasmata is clear, and similar to what happens elsewhere, but the original mode of union of the two pre-optic limbs is not possible of observation at this stage. The connection of the more anterior of these pre-optic limbs with the hinder part of the nasal capsule seems to be a carnivorous feature. The exoccipital cartilage, projecting as it does backwards with little or no connection with the neighbouring cartilages, is a great help to the proper understanding of that structure.

The supraoccipital cartilage has too a very simple and typical form, and its share in the production of the tectum cranii posterius is very interesting. The existence of a tectum cranii anterius, placed so far forward as it is, and consisting of four parts arranged in the same coronal plane, is likewise a point of very great interest. The small size of the cochlear capsules in comparison with those of the cat is another point of note. The extremely simple form of the ala temporalis too is another interesting point, but it is possible that at a later stage it may become more complicated.

As regards the nasal capsule, the small size of that part which contains the ethmo-turbinals is a feature which is retained up to adult life and almost characteristic of the seal group, in which it is known that the ethmo-turbinals are small and occupy but a small part of the interior of the osseous nose. On the other hand, the large size of the maxillary prominence and corresponding maxillary recess seem to be in harmony with what obtains in the adult condition, but at this stage the maxillo-turbinal cartilage is very small and not even inrolled, whereas in the adult it is of very great size and complexity. There is at this stage no sign of a cartilaginous naso-turbinal. This too is usually a large structure in the Phocidæ in adult life. The condition of the lamina transversalis posterior, the absence of an intermediate segment to the lamina transversalis anterior, are to be regarded as indicating a high stage in phylogeny. The small size of the anterior paraseptal cartilage is clearly due to the absence of an organ of Jacobson.

As to the ancestral history of the animal and the group to which it

belongs, and further, as to its affinities, this communication helps but little. As regards the former, not at all perhaps; as regards the latter, it is impossible to say more than that in certain particulars, *e.g.* the relation of the ala orbitalis to the nasal capsule and the form of the pars trabecularis, together with the presence of well-marked and separate trabeculo-cochlear commissures, a well-marked chordo-cochlear commissure with a large basi-cochlear fissure, the seal resembles the cats, but I do not know how it compares with the Arctoidea in these respects.

The following, taken directly from Weber, 1904, p. 551, is of interest:—

"Vorgeschichte. Die Paläontologie wirft bisher keinerlei Licht auf die Vorgeschichte der Pinnipedia. Es ist zwar eine Anzahl derselben bereits aus dem Miocän bekannt; diese meist unvollständigen Reste schliessen sich aber, insoweit sie sich beurteilen lassen, in erster Linie eng an unsere heutigen Phocidae an. Früher bereits wurde die Ansicht geäussert, dass die Pinnipedia direkt von Creodonta abzuleiten wären. Wenn man dabei auf die geringe Zahl der 1. wies, da ja auch bei Creodonta I.—fehlen kann, so vergass man wohl, dass dies bei Pinnipedia dichtbar, ein Verlust ist, der erst seit Jüngerer zeit, seit Anpassung an das Leben im Wasser datiert. Neuerdings führt Wortman die Pinnipedia auf + *Patriofelis* und damit auf die + Oxyaenidae zurück, welche für den einen noch Creodonta sind, für andere bereits Carnivora, die den Katzen sich nähern. Dieser Ansicht Wortmans ist aber sowohl Winge als auch Osborn entgegengetreten. Ein zusammenhang der Pinnepedia mit den Ursidae ist wohl die gesichertste Annahme. Vergleichung der recenten Formen lehrt eine menge auffallender Uebereinstimmungen kennen, die auf Blutverwandtschaft deuten. Ich nenne den Bau der Trommelhöhle, das Verhalten des Maxilloturbinale, das in beiden ästig ist (Hypomycteri); den langen Darmkanal ohne Flexura duodeno-jejunalis, der an einfachem Mesenterium commune aufgehängt ist; die gelappten Nieren, das Fehlen der Cowperschen Drüsen. Damit kommen wir zum Schluss, dass die Pinnipedia mit den Ursidae zusammen primitiven Amphicyon-artigen Carnivora entsprangen und allmächlich auffällige Umfornung durch ihre Lebensweise erfuhren."

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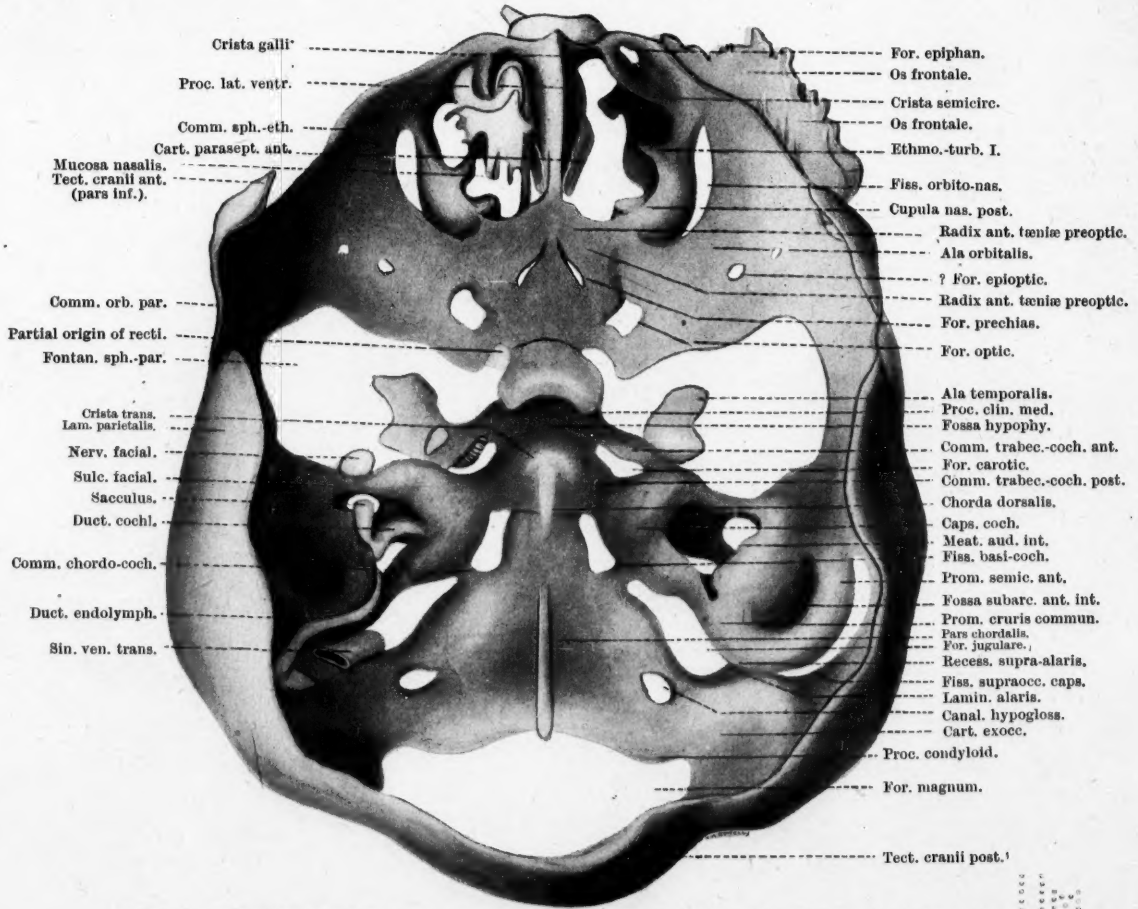
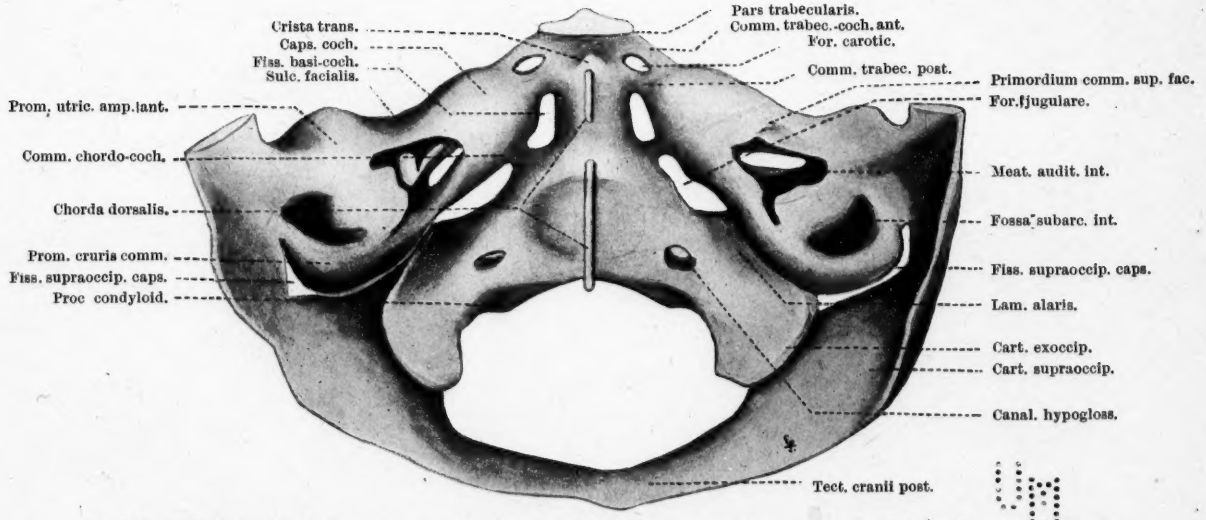
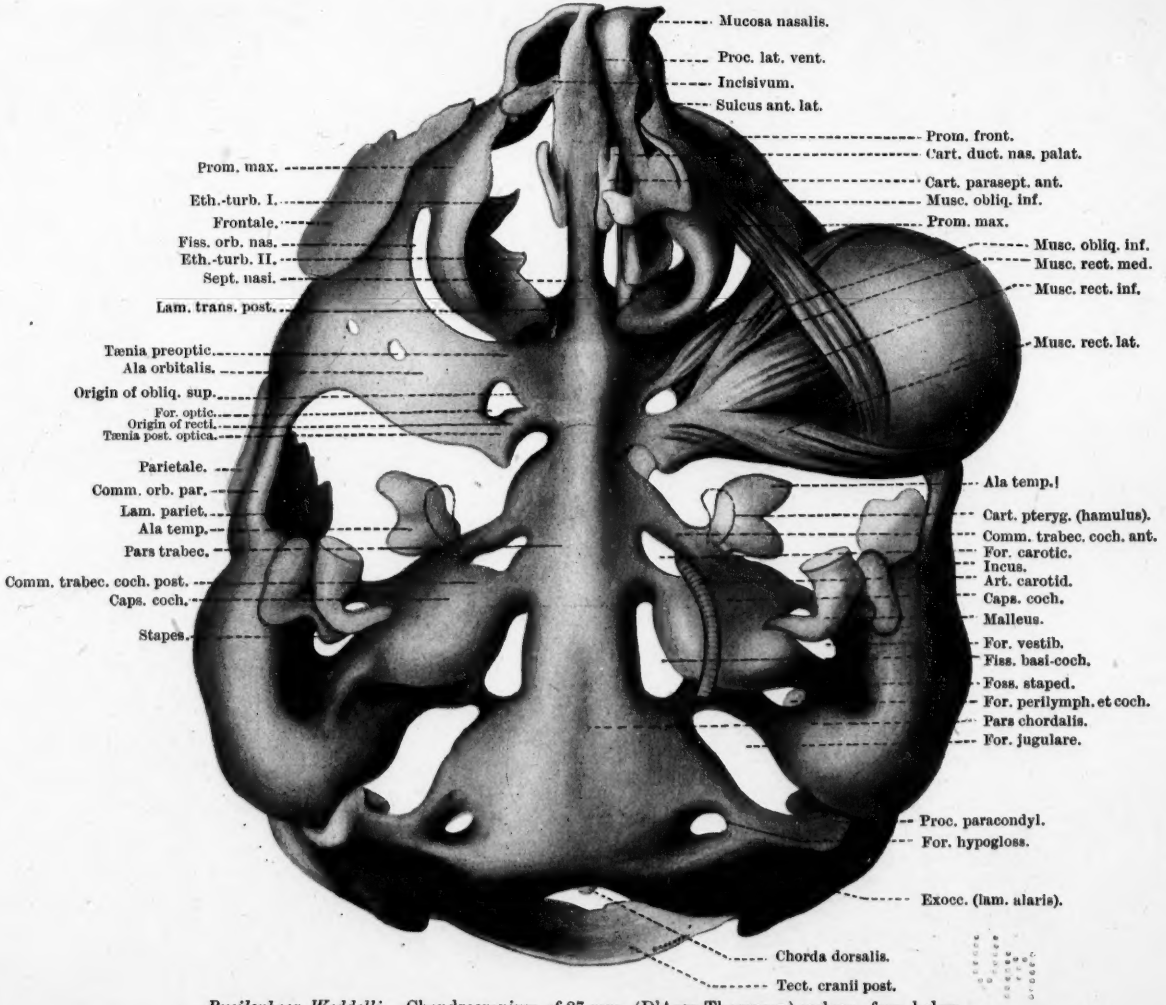


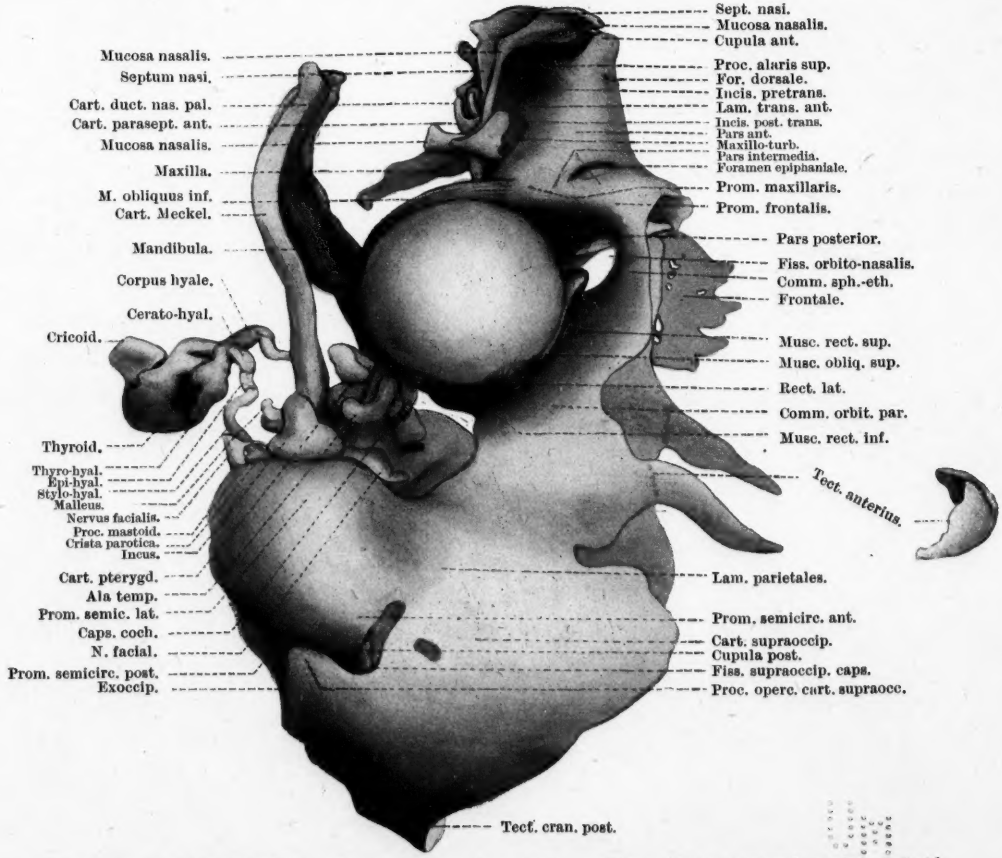
Pœcilophoca Weddelli (Weddell's seal). Chondrocranium of 27-mm. (D'Arcy Thompson) embryo, from above.



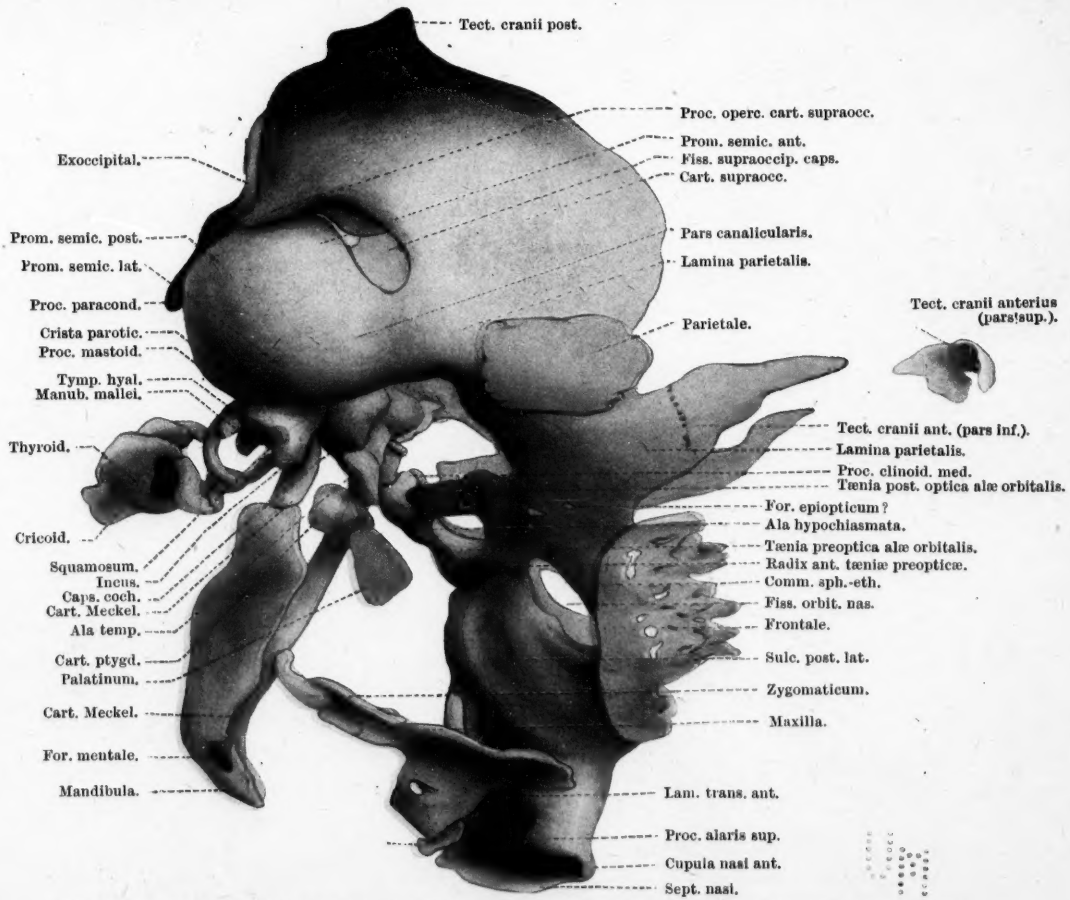
Pœcilophoca Weddelli (Weddell's seal). Caval aspect of hinder half of chondrocranium of 27-mm. (D'Arcy Thompson) embryo, showing especially the exoccipital cartilages.



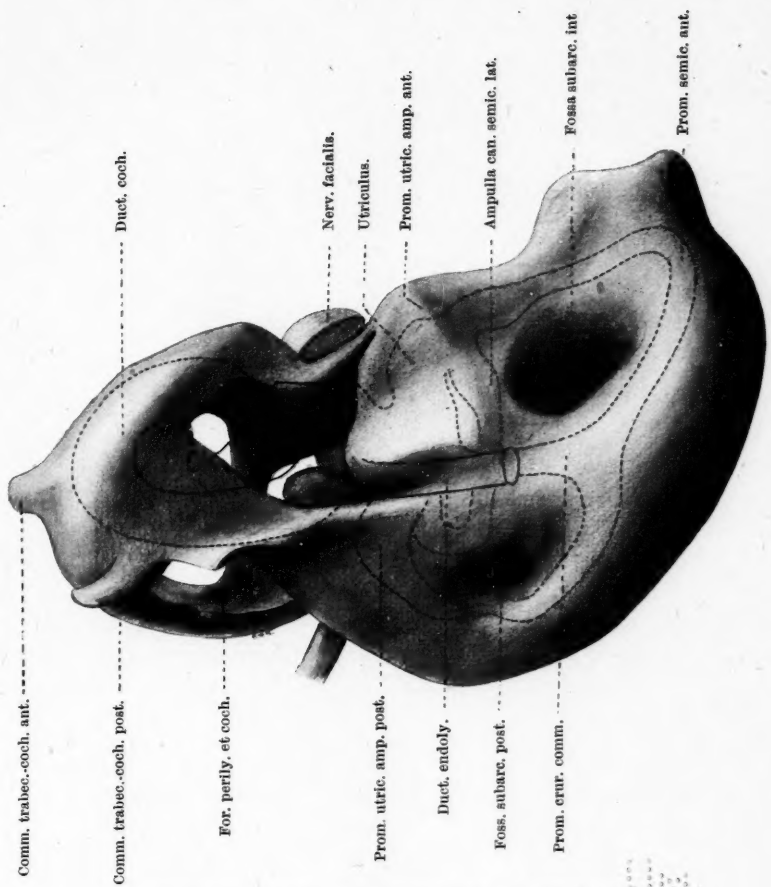
Pœcilophoca Weddelli. Chondrocranium of 27-mm. (D'Arcy Thompson) embryo, from below.



Pœcilophoca Weddelli (Weddell's seal). Chondrocranium of 27-mm. (D'Arcy Thompson) embryo, from left side.



Pœcilophoca Weddelli (Weddell's seal). Chondrocranium of 27-mm. (D'Arcy Thompson) embryo, from right side.



Pœcilophoca Weddelli. Right auditory capsule, from behind.

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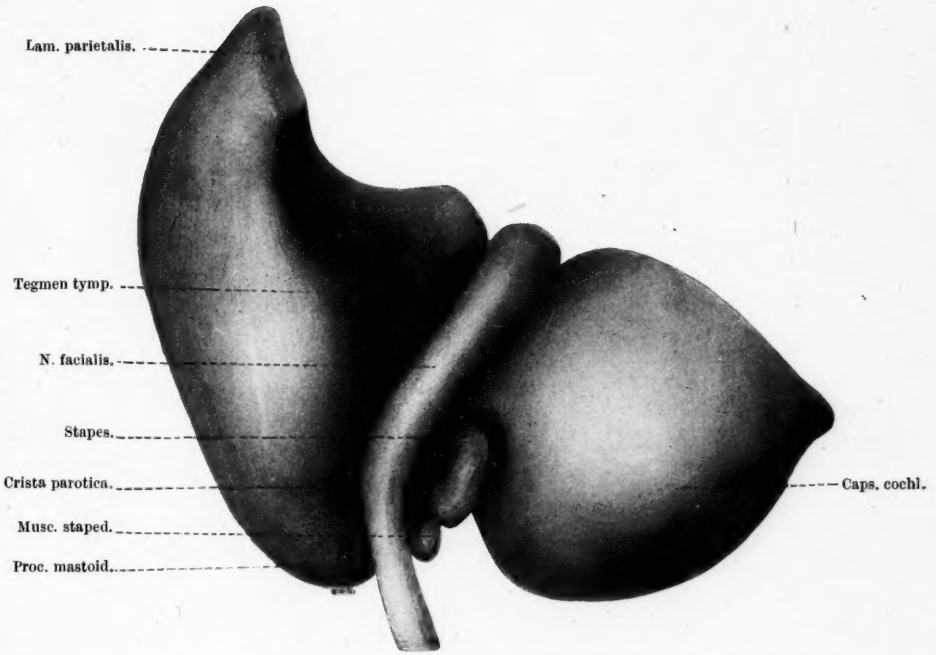

Pœcilophoca Weddelli. Right auditory capsule, from front.

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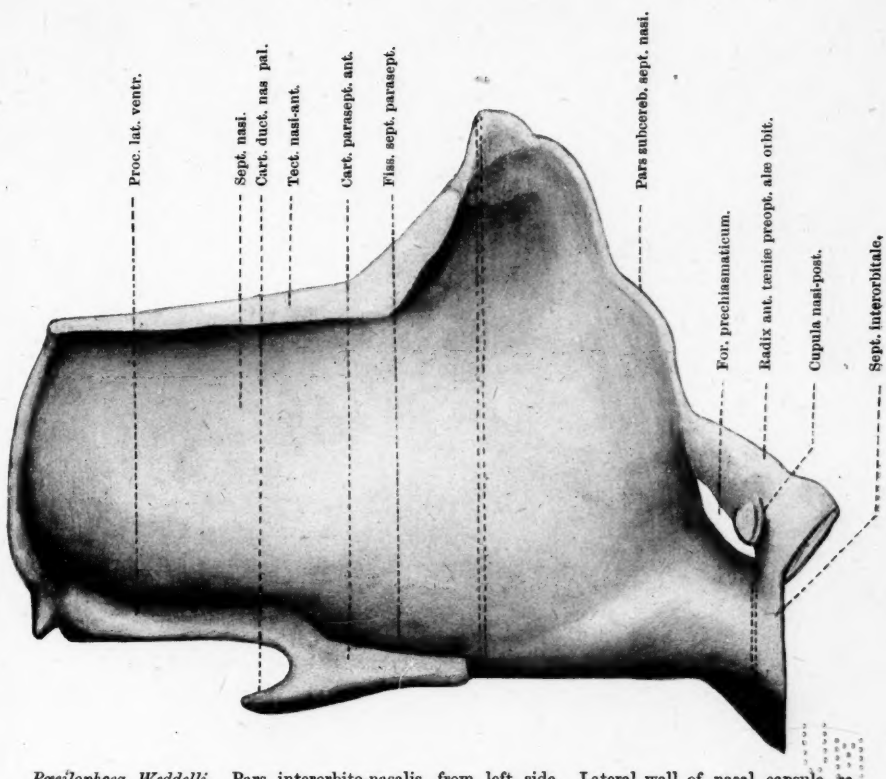

Pœcilophoca Weddelli. Pars interorbito-nasalis, from left side. Lateral wall of nasal capsule removed. The area between the anterior and posterior double interrupted lines is the subcerebral part of the septum nasi.

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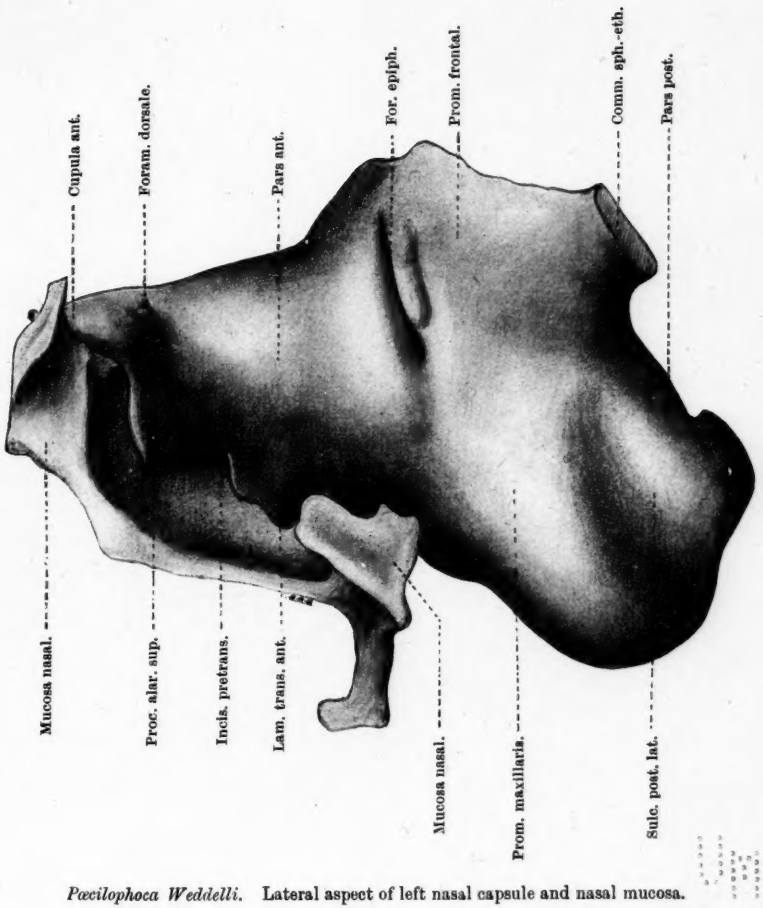

Pœcilophoca Weddelli. Lateral aspect of left nasal capsule and nasal mucosa.

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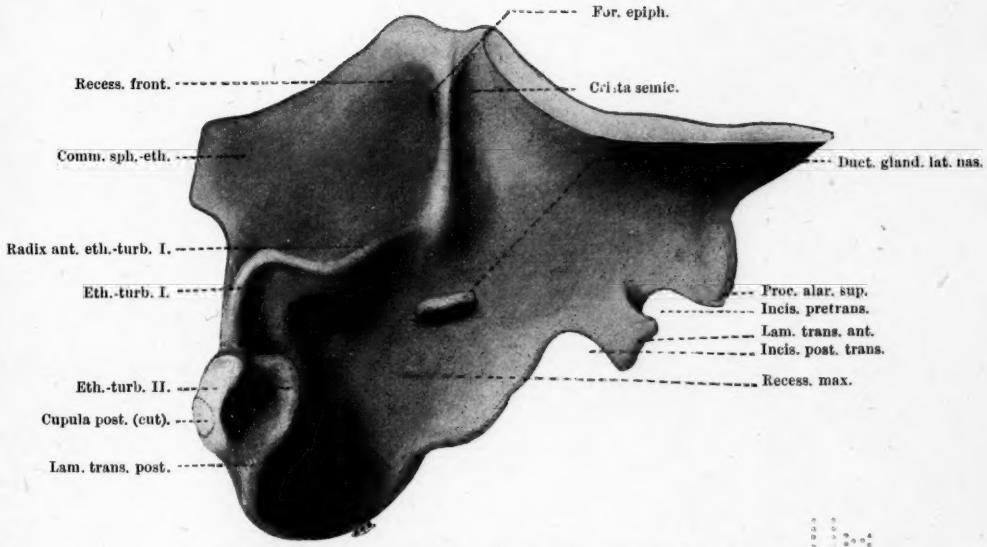

Pœcilophoca Weddelli. Medial aspect of left lateral wall of nasal capsule.

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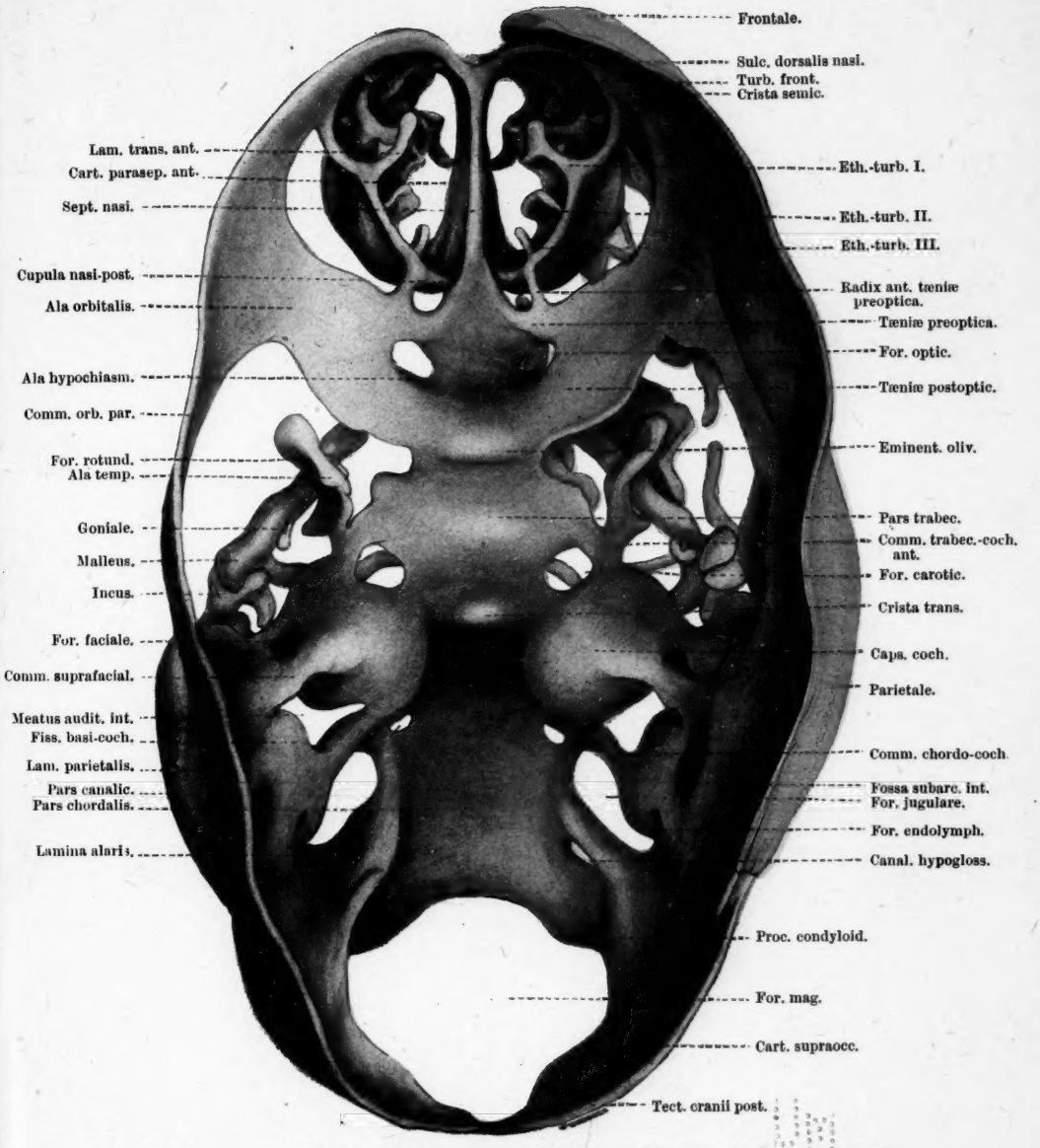

Mustela domesticata (ferret). Chondrocranium of 30–32-day (Robinson) embryo, from above.

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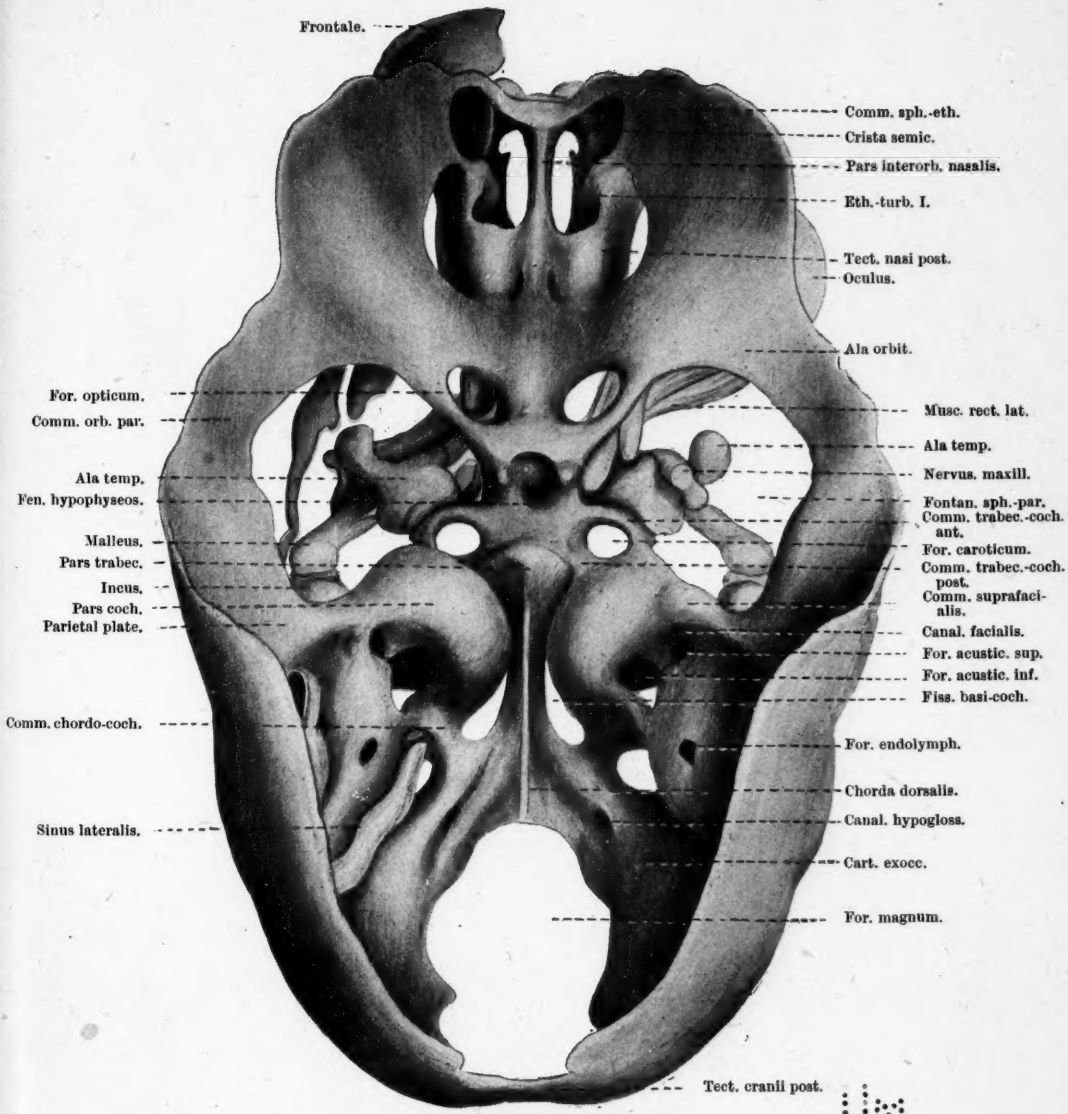

Felis catus. · Chondrocranium of 32-mm. (Hill) embryo, from above.

Professor EDWARD FAWCETT.

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FAWCETT, "The Primordial Cranium of *Erinaceus europœus*," *Journal of Anatomy*, vol. lii.

MACKLIN, "The Skull of a Human Fetus of 40 mm.," *American Journal of Anatomy*, vol. xvi., No. 4, Sept. 1914; vol. xvi., No. 3, July 1914.

CORRIGENDA TO PAPER ON ERINACEUS EUROPÆUS, VOL. LII.

P. 211, l. 3, *read* "19" *for* "25."

P. 242, l. 33, *read* "lamina transversalis posterior" *for* "posterior paraseptal cartilage."

P. 247, l. 4, *read* "19" *for* "25."

ON THE STRUCTURE OF THE HUMAN SOLEUS MUSCLE.

By Douglas G. Reid, M.B., Ch.B., Edin., M.A. Trin. Coll. Cam.

Quain, Poirier, and others give fairly good accounts of the general structure of soleus. Frohse and Fränkel in *Bardeleben's Anatomy*, 1913, deal in some detail with the innervation of this complex muscle, and have even ventured to enumerate the anastomoses which are to be found in its substance between the branches of the two nerves of supply.

Le Double and others deal with the grosser variations of the muscle in man and other vertebrates.

But nowhere can I find mention of the points to which I here especially refer.

One muscle, which I noted whilst superintending dissection, is profoundly modified (see C, fig. 2). In fig. 1[1] the anterior (deep) surface of a practically normal soleus is shown, and the student is recommended to reflect the muscle as is here indicated, viz. by dividing its tibial head.[2] Indeed this head is the (relatively) recently acquired portion of the muscle, and is almost a human characteristic. It is the head incised by the surgeon in the high operation of ligature of the posterior tibial artery.

In this way the nerve which arises from the upper part of the posterior tibial (see fig. 1) and supplies the "anterior" or "fishbone-like" portion of the muscle is not liable to be injured.

A, in fig. 2, also shows the structure of the normal soleus. It is the appearance seen on transverse section at the level of the line in fig. 1, and in B, fig. 2, indicating the central tendon of the fishbone-like part.

In the anomalous muscle C (see fig. 2) a tendinous lamina ((*a*) in figure) lies in the substance of the muscle, reaching practically to its tibial border.

[1] In the original the foot is also shown, for, as in other of my anatomical drawings, I have tried here to get connection between parts in different regions. It has well been said that the illustrations in the books too often fail to show the continuity between different parts of the same structure. In the original the relations of the plantar vessels and nerves to one another are shown. The external plantar artery nowhere directly "lies upon the calcaneum." It is separated from its inner surface by the flexor hallucis longus tendon, the external plantar nerve, and flexor accessorius. Fig. 1 was prepared from a drawing made upon a varnished glass plate held over the specimen.

[2] This is the method which I find is now advised in *Cunningham's Practical Anatomy*, as revised by Robinson.

It is formed largely of longitudinal fibres, and becomes continuous with a tendinous sheet which extends on the anterior (deep) surface of the muscle to the upper part of its fibular border (see (*b*) fig. 2). From the anterior

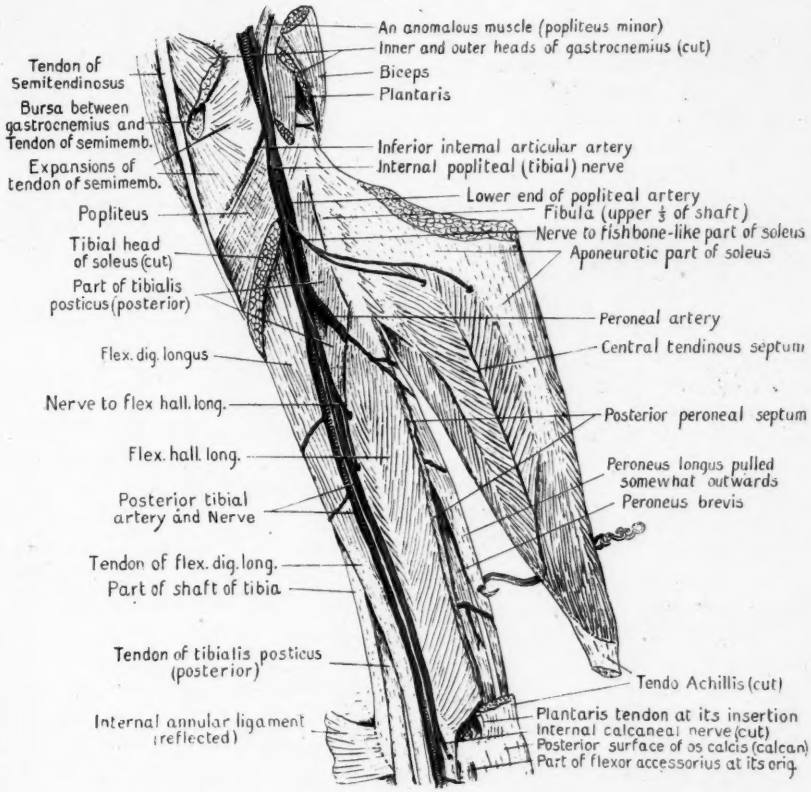
An anomalous muscle (popliteus minor)
Inner and outer heads of gastrocnemius (cut)
Biceps
Plantaris
Tendon of Semitendinosus
Bursa between gastrocnemius and Tendon of semimemb.
Expansions of tendon of semimemb.
Inferior internal articular artery
Internal popliteal (tibial) nerve
Lower end of popliteal artery
Popliteus
Fibula (upper ⅓ of shaft)
Nerve to fishbone-like part of soleus
Tibial head of soleus (cut)
Aponeurotic part of soleus
Part of tibialis posticus (posterior)
Peroneal artery
Flex. dig. longus
Central tendinous septum
Nerve to flex hall. long.
Posterior peroneal septum
Flex. hall. long.
Peroneus longus pulled somewhat outwards
Posterior tibial artery and Nerve
Peroneus brevis
Tendon of flex. dig. long.
Part of shaft of tibia
Tendon of tibialis posticus (posterior)
Tendo Achillis (cut)
Internal annular ligament (reflected)
Plantaris tendon at its insertion
Internal calcaneal nerve (cut)
Posterior surface of os calcis (calcan)
Part of flexor accessorius at its orig.

FIG. 1.—Back of the right leg viewed from behind and above. Soleus has been reflected by dividing its tibial head, and its anterior surface is seen. The venæ comites are not represented.

surface of this lamina muscular fasciculi arise, which course downwards and inwards to end on the fibular (outer) border and posterior surface of another tendinous sheet (see (*c*) fig. 2). It is noteworthy that, in association with the passage of the fishbone-like part generally towards the outer border of soleus, muscular fasciculi usually extend farther downwards along the tibial than along the fibular border of the muscle (see, *e.g.*, E,

fig. 3). The reverse is the case in muscle C; and the fasciculi at the borders of this muscle, at least on its tibial side, do not curve over these in the manner of the short oblique fasciculi that are so characteristic of the normal and very powerful soleus.

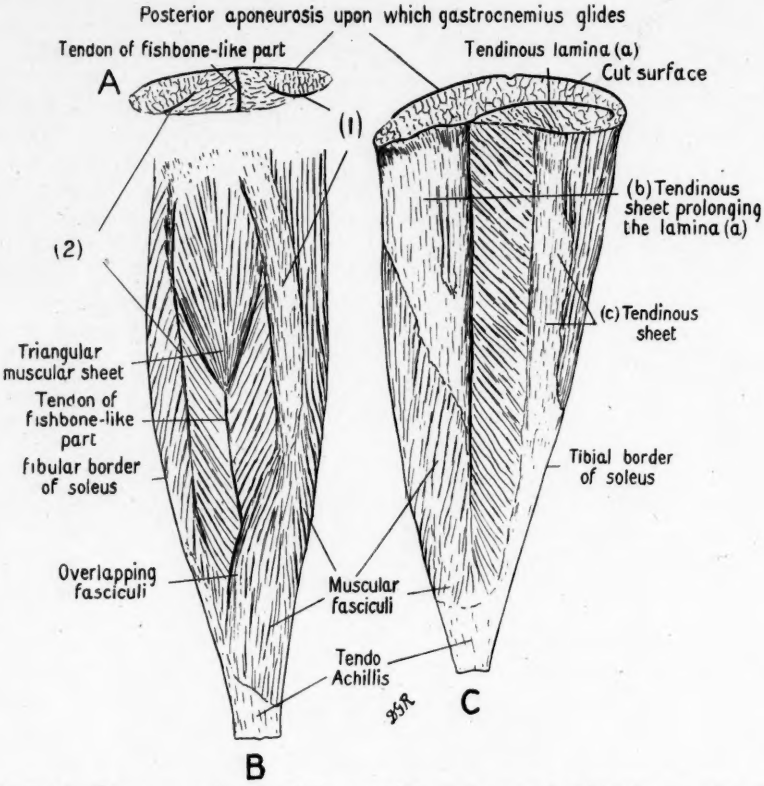

FIG. 2.—A. Transverse section (semi-diagrammatic) of the normal right soleus muscle. B. Slightly abnormal right soleus. C. Anterior surface of right soleus. The figures 1, 2 indicate corresponding parts.

The appearances of the muscle suggest that the fibular lamina 2 (see A and B, fig. 2) has become greatly enlarged, that the tibial lamina 1 is not represented except superficially (see (*c*) in C, fig. 2), and that there is nothing to represent the middle tendinous sheet of the fishbone-like part of the muscle, the fasciculi which arise from lamina 2 extending to be inserted into lamina 1. On the other hand, the relative size, position, and

relations of parts do not suggest this modification; and a muscle which is so greatly altered is, I think, most noteworthy.[1]

The "anterior," "deep," or "fishbone-like" part presents several other variations. It is sometimes distinctly asymmetrical, and varies considerably in its relative width.

In B (fig. 2) it is modified by the presence of a triangular muscular sheet which conceals the upper part of its "central" tendon. On reflecting this sheet a typical bipenniform part was exposed.

The lower part of the central tendon is also hidden, more or less, in different specimens (see figs. 1, 2) by fasciculi which pass obliquely over it from the tibial towards the fibular side, being inserted into the outer aspect of the "central" tendon as well as into the outer part of the anterior surface of the tendo Achillis. To see the mode of termination of the bipenniform "muscle" these fasciculi must be dissected away.

In other specimens they are absent, and the central tendon is then exposed downwards to its lower extremity.

The tendinous fibres of the fibular lamina (2 in A, B, fig. 2), which in its upper part arises from the posterior surface of the shaft of the fibula (see fig. 1), vary considerably in the extent to which they appear, and extend downwards upon the surface of the muscle to the outer side of the "fishbone-like" part (compare, *e.g.*, figs. 1 and 3).

In three-fourths of the specimens examined the lower part of the fishbone-like portion ("muscle") approaches distinctly closer to the outer than to the inner (tibial) border of the muscle. It may extend actually on to this border (see, *e.g.*, E, in fig. 3). Indeed its "central" (middle) tendon may pass below into continuity with the fibular border of the tendo Achillis, and the muscle becomes penniform in its lower part (see E, fig. 3).

In one-fourth of cases, as in muscle D (fig. 3), the "fishbone-like" part extends below on to the *tibial* border, and in this case it becomes penniform below on the reverse side. The penniform part, together with the oblique fasciculi which spring from the same tendinous sheet (2, see fig. 3), then give rise to a sort of bipenniform process, and the muscle may appear as if it had been sliced down on the lower part of its tibial aspect (see D, fig. 3).

In the soleus shown in fig. 1 the central tendon passes first towards the fibular side of the muscle and then becomes bent, so that its lower part, covered by the overlapping fasciculi referred to, passed to end near the tibial border of the tendo Achillis. Only in one in sixteen specimens

[1] In one specimen the inner half of the "fishbone-like" part is covered by longitudinal tendinous fibres, and, without care, what is really a bipenniform muscle might have been described as penniform. These tendinous fibres are a prolongation of the posterior border of the central tendon. Compare this with E, fig. 3.

does the central tendon end exactly on the middle line of the tendo Achillis, and the muscle is remarkable for its great symmetry.

In many cases the "central" tendon is practically an antero-posterior septum (as is seen in the section of the normal soleus A, in fig. 2) in connection with the posterior aponeurosis and the tendo Achillis, and coming to the anterior surface of the muscle by its anterior border. In other cases

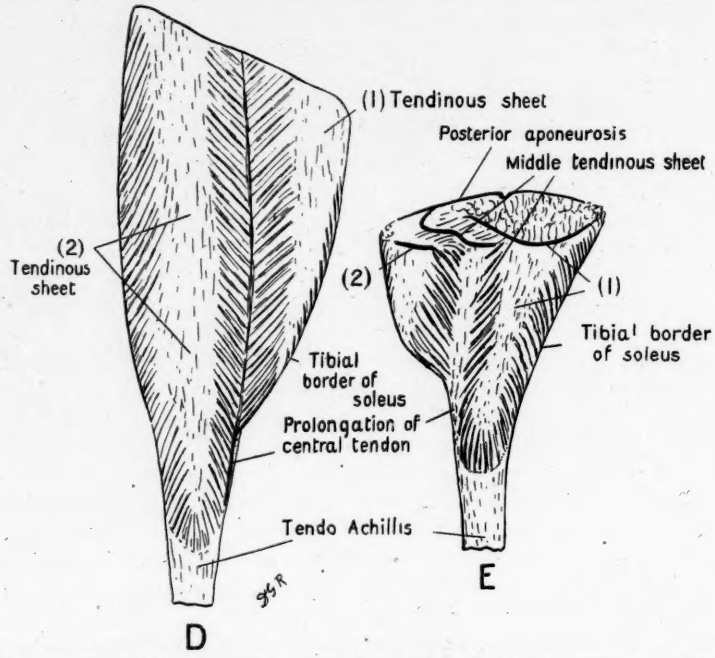

FIG. 3.—Two right soleus muscles. D simulates a left soleus muscle. (These drawings were made first upon a varnished glass plate held over the specimens.)

it is distinctly oblique, being directed backwards towards the fibular or sometimes towards the tibial side. It may be distinctly curved. In case E (fig. 3) this middle tendinous lamina lies in a distinctly frontal plane, and comes to the anterior surface of the muscle, not as a mere border, but in the form of a relatively broad strip separating the two parts of the bipenniform muscle from one another. The tendinous sheet after bending on itself is attached to the anterior surface of the posterior aponeurosis, but its lower part becomes continuous with the outer border of the tendo Achillis.

Specimen D (see fig. 3) presents an arrangement which is just the

reverse of that presented by specimen E. In both there is the bipenniform process already mentioned. In E the muscle appears as if it had been quite abruptly sliced down on its fibular border. This appearance of slicing down is seen also in D, but is not so marked. It is correlated with the abrupt encroachment of the "fishbone-like" part of the muscle on the border of soleus.

The muscle looks distinctly lop-sided in E; and it is noteworthy that the outer head of gastrocnemius related to E, and which is as broad but not quite as thick as the inner head, descends somewhat lower than the inner head.

This is possibly a correlated variation, and should be looked for in specimens in which there is a marked "slicing away" or notching.

Anyone would quite readily have mistaken the gastrocnemius as belonging to the left leg.

But marked cutting away is not generally to be found. Indeed the other muscles specially examined present little or no indentation of their borders (see also figs. 1, 2).

The tibial tendinous lamina (1) is better developed in E than is usual, whilst, apparently as a variation correlated with the form and direction of the central or middle tendinous sheet (see fig. 3), the fibular tendinous lamina (2) does not extend into the substance of the muscle. The muscular fasciculi take origin from its inner border and posterior surface only.

It is most noteworthy that a soleus muscle may present an arrangement which is just the reverse of what is normal, and unless careful one could readily mistake the side to which the muscle belongs.

In this paper, then, I have merely touched upon the question of the architecture of soleus and a related muscle and their correlated variations.

This question, however, opens up a very large field for research to anyone who is observant in the course of the dissection of the human body and who keeps in mind the truly memorable words of Cuvier—"single parts cannot change without bringing about modifications in the other parts."

I have indicated, what seems obvious, that there are variations which may be *compensatory*—a "cutting away" supplied by some addition elsewhere; and one must try ever to render variations *of any kind* intelligible by determining, as far as possible, the mechanical causes which really operate in producing them.

Comparative anatomy also may help us to see the mechanical causes at work in the case of "atavistic" variations.[1]

[1] Haughton's *Principles of Animal Mechanics* (Longmans, Green & Co.) will be found useful to those interested in the mechanical advantages of such arrangements of muscular fasciculi as those referred to in this paper.

It will be seen that the examples of the soleus which I have described may be arranged into the following groups:—

(1) Symmetrical forms.
(2) Forms in which the bipenniform part ends on the fibular side of the muscle.
(3) Forms in which it ends on the tibial side.
(4) Forms in which its tendon is concealed below by overlapping muscular fasciculi, or
(5) Above by a more or less triangular muscular sheet.
(6) Forms in which its central tendon appears as an edge on the anterior surface of the muscle.
(7) Forms in which the tendon, which may be distinctly curved, appears on the surface as a lamella which occasionally is prolonged over one-half of the "muscle."
(8) Forms in which there is a penniform muscle.

THE HOMOLOGY OF THE MAMMALIAN ALISPHENOID AND OF THE ECHIDNA-PTERYGOID.

By H. Leighton Kesteven, D.Sc., M.B., Ch.M.

I. The Homology of the Mammalian Alisphenoid.

The Argument in Brief.

(1) The alisphenoid of the Crocodile can be shown to be developed from a true otosphenoidal plate.
(2) In Sphenodon both otosphenoidal plate and epipterygoid are present.
(3) The Crocodilian alisphenoid is therefore not an epipterygoid.
(4) It is therefore clearly erroneous to quote the Crocodilian condition in support of the alisphenoid-epipterygoid homology.
(5) That homology having definitely been disproven in this case, the theory is thereby weakened.
(6) There is reason to believe that the Cynognathid epipterygoid lying lateral to the Gasserian ganglion was not a true cranio-mural element, but, as in the Chelonians, was a pseudo-mural element, the true wall being membranous and medial to the ganglion.
(7) There is little doubt that the alisphenoid of the Ophidians is absolutely homologous with that of the Crocodile.
(8) There is every reason to regard the relation of the Gasserian ganglion to the cranial bones and the situation of the first branch of the fifth nerve as features whose importance has been overstated.
(9) In one case at least (*Python spilotes*) the Gasserian ganglion lies medial to the alisphenoid.
(10) Among the Theria the Gasserian ganglion lies as often medial to the otocrane as medial to the alisphenoid.
(11) There is no doubt about the homology of the otocranial elements of Reptiles and Therians, and that the ganglion has somehow come to lie medial in the Therians whereas it was lateral in the Reptiles.
(12) Why doubt the homology of the alisphenoids in the two groups?
(13) Other nerves besides the first branch of the fifth have intracranial courses in one or more cases and extracranial in others:—

(*a*) The sixth nerve in most if not all Lacertilia, Ophidia, and Chelonia runs an extracranial course from posterior to the sella.

(*b*) In the birds this nerve runs an intraosseous course lateral to the sella.

(*c*) In the Therians it is intracranial to well in front of the sella.

(14) Is not this an illustration of how a nerve may become intracranial as the shape of the brain case alters?

(15) In *Perameles obesula* the second and third branches of the fifth nerve have an intracranial course almost as lengthy as that of the first branch, yet there can be no suggestion that it is not the alisphenoid they lie on.

(16) The embryological evidence adduced in support of the alisphenoid epipterygoid homology, when viewed correctly, is found to remove what might have been a vital objection to regarding as homologous the alisphenoids of Reptiles and Therians.

(17) The Reptilian alisphenoid is developed from the otosphenoidal plate.

(18) The otosphenoidal plate is a parachordal derivative.

(19) The basipterygoid process is a trabecular derivative.

(20) The ala temporalis has an origin independent of the processus alaris.

(21) The processus alaris is the Mammalian homologue of the Reptilian basipterygoid process.

(22) The cartilaginous ala temporalis may be regarded as a remnant of the disintegrated otosphenoidal plate.

(23) In one case at least (Trichosurus) the ala temporalis has primitively complete independence of the processus alaris and trabeculæ.

There are then no valid arguments against the correctness of the older view that the alisphenoids of Reptiles and Mammals are homologous, and it follows that the alisphenoid of Birds is homologous with both.

The Discussion.

The history of the development of the alisphenoid in *Crocodilus johnsoni* is as follows:—

Stage 1 (length 25 mm.).—The chondrocranium has at this stage reached its full development, none of its elements shows any ossification, whilst the covering bones are more or less ossified, as also are the membrane bones of the craniovisceral skeleton (fig. 1).

Immediately in front of the otic capsule is the oval foramen prooticum, which transmits the roots of the fifth nerve; in front of this is a rod

of cartilage, continuous above and below the foramen with the capsule. Below, this rod is also continuous with the cartilaginous basis cranii lateral to the posterior end of the sella; anteriorly, it is attached to the membrana spheno-obturatoria. The pterygoid articulates with it both above and below the foramen prooticum.

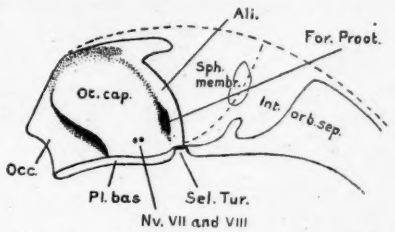

FIG. 1.—*Crocodilus johnsoni.* Chondrocranium seen from within.

Stage 2 (length 40 mm.).—The ossification of the whole skull is nearing completion (figs. 2 and 3).

The bar in front of the foramen prooticum, like all the other cartilages,

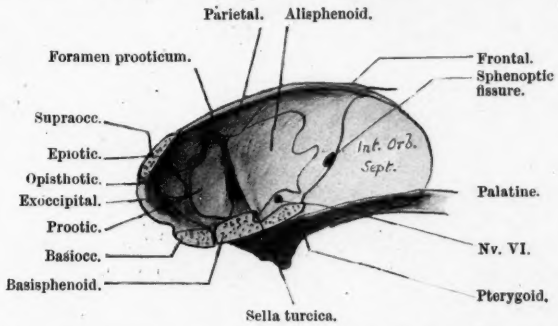

FIG. 2.—Side wall of cranium of young crocodile to show the extent and relations of the alisphenoid.
The sphenoptic fissure transmits the structures usually transmitted through the sphenoidal and optic fissures, except the first branch of Nerve V., which arises in the foramen prooticum in this case.

is ossified, and there is an extensive ossification of the membrana spheno-obturatoria spreading forward from it. This with its superadded membrane bone is the alisphenoid; its relations are as follows: Below, it articulates medially with the postclinoid eminence of the basisphenoid medially and with the pterygoid externally. Viewed from within it is found to articulate posteriorly with the prootic below, above this to form the anterior

boundary of the foramen prooticum, above this it articulates with the prootic a second time, along the roof it articulates with parietal behind and frontal in front. Viewed from without, immediately behind the articulation with the pterygoid, the alisphenoid articulates with the quadrate; above this articulation the prootic and the foramen prooticum separate quadrate and alisphenoid, which meet again above the foramen; along the roof are the articulations with parietal and frontal.

The Gasserian ganglion is found lying against the cartilaginous rod and membrana spheno-obturatoria in Stage 1, and in a fossa on the outer aspect of the alisphenoid just in front of the foramen in Stage 2.

A comparison of my Stage 1 with stages Q and R of Sphenodon, as

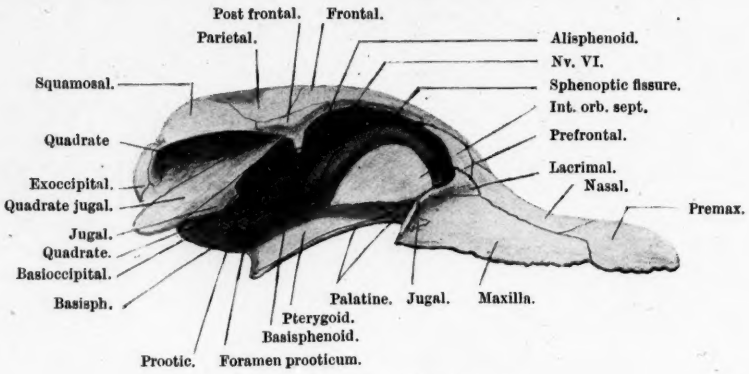

FIG. 3.—Young *Crocodilus johnsoni*.

figured by Howes and Swinnerton (1), pl. iii. fig. 4 and pl. iv. fig. 10, can leave no doubt that the cartilaginous rod which has been described above is represented by the body and process 4 of the otosphenoidal plate; that is, that the alisphenoid of the Crocodile is developed from an otosphenoidal plate.

On pl. iv. fig. 3 in the same work the otosphenoidal plate is shown in transverse section, with the epipterygoid lateral to it and separated by nerve elements below, which are probably Gasserian ganglion; the first branch of the nerve is definitely indicated medial to the epipterygoid and lateral to the otosphenoidal plate.

Quite apart from the situation of the ganglion and nerve, however, a comparison of the two leaves one convinced that the alisphenoid of the Crocodile, being developed from an otosphenoidal plate, cannot be regarded as a modified epipterygoid.

Broom, who in 1907 (2) expressed the opinion that we are justified in assuming that the alisphenoid of Mammals is homologous with part of the cartilaginous pterygoid arch of the Reptiles—thereby giving birth to the epipterygoid-alisphenoid homology theory—at that time proposed to regard the alisphenoid of Crocodiles as homologous with the columella cranii of other Reptiles. He had previously shown that in several diverse orders of the Lacertilia there was actual or presumptive embryological evidence of that cartilaginous continuity of the columella cranii and quadrate which had already been demonstrated by Howes and Swinnerton in Sphenodon.

The alisphenoid in Stage 2, described and figured above, might appear to lend strong support to the idea that it is really homologous with the columella. We have here a bar of bone extending from the pterygoid and basisphenoid below to the parietal above, situated immediately in front of the foramen prooticum, and showing actual contact with the quadrate below the foramen (thus apparently maintaining a condition surely primitive, since it is found in earlier stages in several different Reptiles); finally, this bar is derived from cartilage, and the expanded condition of the whole bone is due to secondarily added membrane bone. On the other hand, this bar has been shown to be developed from a portion of the cartilaginous neural cranium derived from the parachordal cartilages, is absolutely in the same anatomical plane as the inner wall of the otic capsule and the membrana spheno-obturatoria, is continuous below with the cartilaginous basis cranii, is in contact *only* with the quadrate, and ossifies quite indifferently thereof at a later date.

Clearly then, though the epipterygoid homology of the alisphenoid in Crocodiles is an inviting idea, we have to decide against it in the face of the evidence.

Broom is not alone in quoting the Crocodilian condition in support of the epipterygoid-alisphenoid homology, for the same error was made by W. K. Gregory (3) in 1913.

Since the Crocodilian condition has been quoted by two such capable observers as Broom and Gregory in support of the theory, it may now be cited as evidence against, and to that extent the theory is weakened.

Further, inasmuch as the error arose from the study and comparison of adult features, we are justified in being slow to accept evidence of like kind from the palæontological record as weighty, more especially when it is remembered that in the case of the fossils it is impossible to check by dissection the assumed relation of the bones to soft structures.

Watson (4) offers an hypothetical outline of the evolution of the epipterygoids in the Therapsids, this evolution culminating in the Cynognathids, in which there is a "posterior process occupying the position

of a quadrate ramus of the pterygoid, which reaches the quadrate, but passes in front and outside that bone" and "forms the side wall of the anterior part of the cranial cavity." From this last he draws the conclusion that the anterior portion of the cranial cavity "is therefore not homologous with that of other reptiles, but increased by the addition of epipterygoid cavities, is analogous to but not completely homologous with those of mammals." He further says, "that this is so is shown by the position of the process which I have at various times described as a processus anterior inferior of the prootic in the Therapsids. This process forms the lower border of the incisura prootica. It always lies medial to the epipterygoid, leaving a space in which the semilunar ganglion must have lain. . . . The anterior superior process of the prootic of a Cynognathid, which passes inside the upper end of the epipterygoid, forms part of the side wall of the anterior part of the brain cavity."

Now, an examination of the skull of the Crocodile checked by dissection reveals the fact that in all these features the alisphenoid agrees with the Cynognathid epipterygoid, except that the processus anterior inferior prootici, which lies medial to the Gasserian ganglion, is flush with the alisphenoid, there being no space between the two in which the ganglion might lie.

Watson rightly decided that the two bones are not homologous in the presence of this one feature. It will be shown later that though Watson was correct in his conclusion, the evidence on which he relied was untrustworthy.

There can be no doubt that the bone termed epipterygoid in the Cynognathids and Therapsids generally is correctly named; it remains to be proven that it is never a true cranio-mural element.

Watson correctly assumes that the ganglion lay in the interval he describes between the processus anterior inferior prootici and the epipterygoid; he is, however, wrong in assuming that it is therefore intracranial.

In all the recent Reptiles in which an epipterygoid is present the ganglion lies lateral to the inner wall of the prootic and its anterior inferior process when present and medial to the epipterygoid, but outside the lateral cranial wall which, membranous in this region, rises from the basis cranii along the basisphenoid, and prootic anterior inferior process when present toward the sphenoidal flanges of the parietal and frontal bones, the posterior and inferior boundaries of the prootic foramen being bony, the anterior and superior membranous.

Were we unable to check by dissection our observations of and deductions from the Chelonian skulls we would assuredly decide that the Gasserian ganglion and first branch of the fifth nerve are intracranial. In

Chelone midas the ganglion would be correctly assumed to have lain between the post-clinoid process and the processus anterior inferior prootici on the inner side and the epipterygoid process of the pterygoid on the outer, just below the suture with the alisphenoidal lamina of the parietal, and therefore medial to the vestigial epipterygoid, apparently within the cranial cavity. A dissection shows, however, that the true cranial wall is membranous, being attached below to the processus anterior inferior prootici and to the post-clinoid process, extending thence upward and outward to be attached to the alisphenoidal lamina of the parietal well above the ganglion, which thus lies medial to the epipterygoid and lateral to the anterior inferior process of the prootic but outside the cranial cavity. In *Chelodina longicollis* the skull features would lead to similar conclusions, not only the ganglion but also the first division of the nerve apparently lying within the cavity, the latter for the greater part of its length. Here, again, a membranous cranial wall intervenes between the brain and the ganglion. The pseudo-cranial wall is in this case formed by a sphenoidal lamina of parietal above and a much smaller sphenoidal flange of the pterygoid below.

A comparative study of the Reptiles reveals the fact that except in certain specialised forms the true bony brain-box is composed of the elements of the occipital segment, the elements of the otocrane, one or more dorsal membrane bones in front of the supraoccipital, and a basisphenoid below in front of the basioccipital. Laterally in front of the otocrane the wall is or was membranous or cartilaginous, except dorsally, where more or less constantly a sphenoidal flange from the parietal and (or) frontals enters into the cranial boundary.

In all these cases we find: the seventh nerve traverses the otocrane, the fifth leaves the cranium immediately in front of the otocrane, the sixth, fourth, third, and second pass forward with longer or shorter intracranial course to reach the orbit.

It is to be concluded, then, that the primitive brain-case was devoid of components other than those derived from the occipital vertebræ, the basicranial axis, the auditory capsule, and the covering bones dorsally.

In certain specialised forms—Cynognathids, Crocodiles, Ophidians, and Chelonians—we find expanded bony plates actually or apparently bounding the cranial cavity laterally in front of the otocrane.

Dissection of the recent forms discovers to us that these plates are of two quite different kinds, so that we can recognise on the one hand pseudo-mural elements (Chelonians) and true cranio-mural elements (Crocodiles and Ophidians).

The Cynognathid epipterygoid is doubtless a pseudo-mural plate. The

true cranio-mural elements—alisphenoids of Crocodiles and Ophidians—must surely be correctly homologised with the alisphenoid of Mammals.

The Ophidian alisphenoid lies in the side wall of the cranium, flush with the inner wall of the otocrane; like that of the Crocodiles, it articulates with the true basicranial bones below, the prootic behind, and the parietal and frontal above. Together with the prootic it bounds a Gasserian fossa in which the ganglion lies. At the outer end of this fossa are the foramen ovale and foramen rotundum.

Though the ganglion here lies definitely more within than without the cranial cavity, there can be no doubt that the two alisphenoids are homologous.

Believing that the Cynognathid epipterygoid was a true cranio-mural element, Watson concluded that the anterior portion of the cranial cavity was not homologous with that of other reptiles, but had been added to by epipterygoid cavities. This conclusion rests on the assumed intracranial situation of the ganglion and first branch of the fifth nerve, and is in accord with Gaupp's previously expressed ideas.

It has, however, been just shown that the Cynognathid epipterygoid was in all probability not a true cranio-mural element and the ganglion not intracranial, and it is further contended that the true Reptilian alisphenoids are homologous with the Therian alisphenoids.

As against this idea, the only features to which importance is attributed are the intracranial situation of the ganglion and nerve in the Theria.

But it is surely an error of judgment to lose sight of the fact that however or wherever the cartilaginous precursor of the ventral portion of this bone may be found in mammals, the bone itself in its cranio-mural portion is always developed in the sphenoidal membranous side wall of the brain cavity exactly as in the Crocodiles and (presumably) Ophidians.

When, further, it is realised that the relation of the ganglion to the cranial wall is distinctly variable, one must conclude that this is a feature whose value in the present problem has been overestimated.

In the recent Lacertilia and Chelonia the ganglion lies always upon the outer side of the cranial wall. In the Crocodilia it lies embedded in the side wall, the first branch of the nerve passing forward through, not outside, the bone. In the Ophidia (*Python spilotes*) it lies inside the cranial cavity, the first branch leaving the cranium by a veritable foramen rotundum, which is distinct from the foramen prooticum, here a true foramen ovale.

In the birds (Anas, Podargus, Dromæus, Gollus, Meleagris, and Corvus) the ganglion appears always to lie on the floor of the temporal fossa on

the alisphenoid in front of the petrosal, with the foramen rotundum very close to the foramen ovale, and the first branch passing forward through the bone, not upon it.

Among the Mammalia there is a good deal of variation in its relation to the bones in the side wall of the cranium. In Echidna it lies on the ala temporalis, the Echidna-pterygoid, and the prootic. In Ornithorhynchus, Watson's sections show it to lie on the ala temporalis and the anterior process of the prootic. In some Marsupials (Phascolomys and Phascolarctus) it is situated entirely in front of the petrosal; in others (Dasyurus, Trichosurus, Perameles, and Macropus) it is situated farther back, so as to give

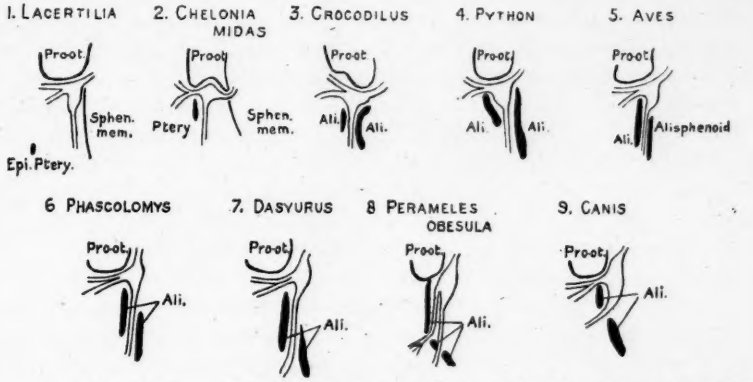

FIG. 4.—A series of diagrams illustrating the varying relation of the Gasserian ganglion and the branches of the fifth nerve to the cranial side wall. Of particular interest are numbers 3, 4, 5, 6, and 7.

Epi ptery., epipterygoid; *pter.*, pterygoid; *proot.*, prootic; *sph. mem.*, sphenoidal membrane.

rise to a shallow furrow on the anterior end of the petrosal. In Tatusia and Edentate the ganglion is situated in a furrow on the medial aspect of the petrosal. In Pteropus I find the ganglion in front of the petrosal. In all other mammals which I have been able to dissect I find the ganglion partially or wholly medial to the petrosal except in the Primates; in these it lies on the upper aspect of the petrosal. These varying situations are shown in the diagrams fig. 4.

In all the Reptiles (except Crocodiles and the Ophidians) the Gasserian ganglion lies lateral to the alisphenoid and sphenoidal membrane, also lateral to the otocrane and in front of it. Among the mammals the ganglion lies commonly medial to the otocrane, and not in front of it. There can be no doubt about the homology of the otocranial elements, therefore it is admitted that somehow the ganglion has come to lie

medial to the periotic bones. Why not to the alisphenoid also? The sixth nerve like the first branch of the fifth has changing relation to the cranial floor in reptiles, birds, and mammals.

In *Chelone midas* I have shown (5) that this nerve perforates the post-clinoid process; that is to say, it leaves the cranial cavity behind the pituitary fossa, and therefore runs an extracranial course almost from its origin. Such is the condition in most Reptiles owing to the marked upward tilt of the brain-case forward of the fossa.

In birds the sixth nerve very generally runs an intraosseous course lateral to the fossa. It does so in all the forms mentioned above.

In the mammals the nerve runs an intracranial course for a considerable distance, usually leaving the cranium in front of the fossa.

It is unthinkable that anyone would claim for the mammalian cranium "subclinoid cavities" which are not present in the reptilian, as evidenced by the extracranial situation of the sixth nerve, yet such a claim would be on all fours with a theory that refuses to recognise as homologous the alisphenoids of Ophidians and Mammals on account of the extracranial situation of the first branch of the fifth nerve in the Ophidians.

In most mammals the second and third branches of the fifth nerve have little or no intracranial course, but in *Perameles obesula* these two pass forward alongside the first branch on the inner side of the alisphenoid to a foramen ovale almost level with the foramen rotundum. This is, however, without significance, for, as in *P. nasuta*, the foramen ovale is, as in other mammals, immediately below the fore end of the ganglion.

Being without significance in connection with the homology of the alisphenoids in the two forms, this variation is of interest in showing that a given nerve may be intracranial in one form and extracranial in another, without any such profound difference in the related bones, as is demanded by Gaupp's theory.

It would appear much more in conformity with probability to assume that as the continually widening brain pushed its side wall out, the first branch of the fifth nerve has come to lie internal to the bone by maintaining the shortest course to its destination.

In the Crocodile, indeed, one seems to be able to recognise the first stage in this process already accomplished. Here the first branch of the nerve is found not outside the bone but tunnelling it from the ganglion in the prootic fossa, directly forward for more than half the width of the bone. In the young (Stage 2, *ante*) this tunnel is represented by a very obvious groove on the outer aspect of the bone. Once a lamina has been formed on the outer side, it is not difficult to imagine that the bone internal

to the nerve should sooner or later become absorbed under the pressure of the expanding brain.

The delicate lamina of bone so constantly present on the two sides of the first branch of the nerve as it lies on the cranial floor in the marsupial cranium, and commonly forming a tunnel for the nerve as it approaches the foramen rotundum, may well be regarded as the remnant of the inner lamina of the alisphenoid. These laminæ are certainly evidence of the osteoblastic tissue internal to the nerve, and the most obvious source of such tissue is certainly the primitive side wall.

Far from lending support to the epipterygoid-alisphenoid theory, embryology definitely disproves it within the Reptiles, and indicates that whereas the Reptilian alisphenoid is developed *ad initio* within the sphenoidal membrane from the otosphenoidal plate, the epipterygoid owes any participation in the cranial boundary entirely to secondary acquisition.

If, then, it is demonstrable that in the Reptiles, in which class the epipterygoid reaches its maximum development, an alisphenoid has been developed quite independently of that bone, one cannot but ask: Why tax our imagination by supposing that the alisphenoid of Mammals is derived therefrom?

Broom advances the condition observed by himself in Trichosurus, and Watson adds the conditions found by Wincza for the cat, dog, and bear, by Levi, Gaupp, and Fawcett for man, and Noordenboos for the mole, in support of the alisphenoid-epipterygoid homology.

These investigators have shown that the extremity of the ala temporalis is distinct from or ossifies independently of the processus alaris. Gaupp has advanced reasons which justify us in regarding the processus alaris as homologous with the Reptilian basipterygoid process. (The restriction of Gaupp's conclusions to the processus alaris is correctly maintained by Watson (*loc. cit.*).) In Trichosurus, Broom has shown that the extremities of the alæ temporales first appear as small cartilaginous rods lateral to the trabeculæ and not united in any way with the rest of the chondrocranium; later these rods become attached to the trabeculæ, and are continued upward between the two main branches of the fifth nerve, to be later added to by intra-membranous ossification.

The condition is compared with that described by himself in Chameleo; but unless Chameleo differs fundamentally from Lacerta, the two are not comparable, for whereas in Trichosurus there are no cranio-mural anlagen medial to the ala temporalis rod above the basicranial plane, in Chameleo there is the whole of the otosphenoidal fenestrated cartilaginous plate between the epipterygoid and the brain.

It is in no way surprising that the alisphenoid in Mammals grows upward from the basicranial plane, for it is thus that apparently all cranial elements take origin throughout the vertebrate series above the fish. There is no reason to doubt that the otosphenoidal plate which ossifies to form the alisphenoid in the Crocodile had an origin similar to the otosphenoidal plate in Sphenodon—that is, as an outward and upward growth from the basicranial axis.

The independent origin, and separation from the trabecular cartilage, of the ala temporalis may be regarded as resulting from the fact that it is a derivative of the parachordal cartilage which has undergone profound and more or less disintegrative modification as it appears in the Therians.

Contrariwise, were it possible to show that the alisphenoid of Mammals originates from the processus alaris, then indeed would it be proven otherwise than homologous with the alisphenoid of Reptiles, for, as already stated, there is reason to regard the processus alaris as homologous with the Reptilian basipterygoid process. This latter is developed from the trabecular cartilage, while the Reptilian alisphenoid, ossifying in the otosphenoidal plate, is a parachordal derivative.

It has been stated that the tænia clino-orbitalis of Echidna and Ornithorhynchus are really homologous with and remnants of the reptilian cranial side wall. Whether this be so hardly touches the present discussion; their true homology can only be discussed when we are in a position to decide whether they are ethmosphenoidal (as seems probable), trabecular, or otosphenoidal in origin.

The conclusion the foregoing discussion leads us to is that the alisphenoid bones of the Crocodile, the Ophidia, and the Mammalia are homologous bones, and it follows without argument that the alisphenoid bone of the Birds is homologous with both.

II. The Homology of the Echidna-Pterygoid.

Watson (*loc. cit.*) remarks of the prototherian skull: "The absence of the alisphenoid in the side wall of the cranial cavity is a very remarkable difference which alone makes the monotreme skull differ far more greatly from that of any Therian than the members of the latter group do among themselves." He was, however, struck with the similarity of the Echidna-pterygoid and the tympanic wing of the alisphenoid of Marsupials, and he proposed to regard them as homologous structures.

In this proposal Watson is undoubtedly correct, and in support thereof descriptions and drawings of the bones are here offered.

In Macropus (figs. 5 and 6) the tympanic wing may be described as

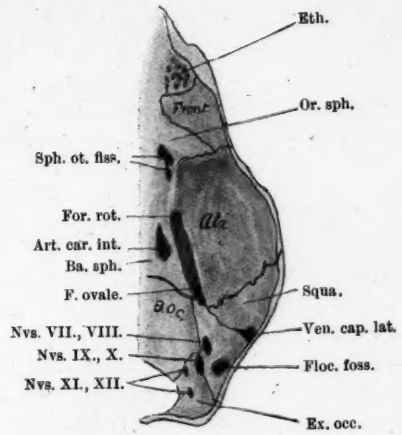

FIG. 5.—Macropus. Right half cranial cavity.

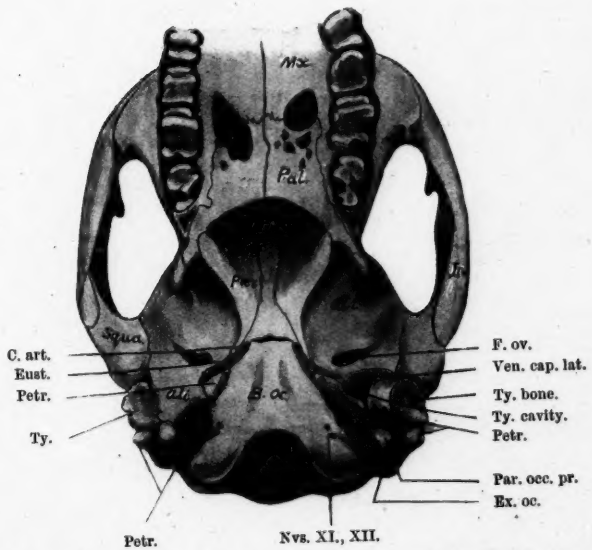

FIG. 6.—Macropus. On the right of the figure the tympanic wing has been removed to show the relation of the bones above it.

that portion of the bone lying behind the anterior boundary of the foramen ovale. Anteriorly it articulates with the basisphenoid medially, and with the squamosal laterally. Lateral to the foramen it forms a portion of the cranial floor. The inner boundary of the foramen is formed by a spur of the bone. Extending backwards it passes beneath the petrosal, sending dorsally on its inner side a flange which articulates with the inner descending wall of the tympanum. In this region it forms the floor of the tympanum, and articulates with the tympanic bone laterally. Behind

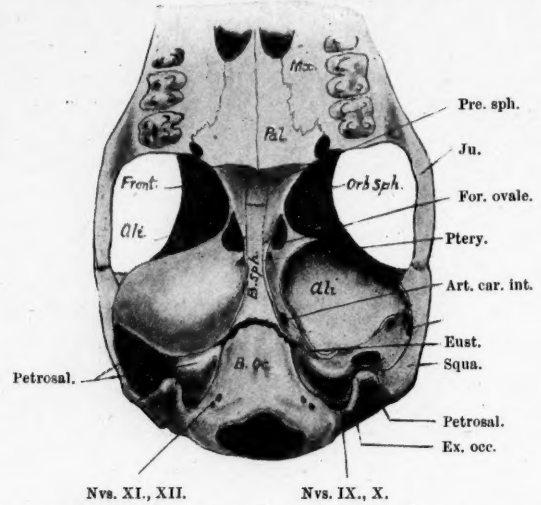

FIG. 7.—*Perameles obesula*. The tympanic bulla has been opened in fig. 7, and in fig. 8 its limit is shown by a dotted line.

the tympanic bone there is an articulation with the petrosal, and medial to this with the paroccipital process of the exoccipital.

In *Perameles nasuta*, lateral to the foramen ovale the wing forms the whole of the front half of the tympanic cavity including the roof, the temporal tegmen being lateral to this and behind it, a small spur from the petrosal intervening. The tympanic bone is to its outer side. The wing is bounded behind by the petrosal, and there is no articulation with the exoccipital.

The condition in *Dasyurus maculatus* is so similar to *P. nasuta* as to need no separate description.

In *Perameles obesula* (figs. 7 and 8) the very large size of the alisphenoidal bulla tympani has thrown the foramen ovale forward almost

level with the foramen rotundum. The roof of the bulla supplies an extensive area of the cranial floor, extending from the basioccipital and basisphenoid right to the side wall. On the cranial floor the alisphenoid and squamosal do not meet; they are separated by a spur of the petrosal, which also separates the alisphenoidal bulla from the squamosal tegmen tympani, and at the same time forms the inner half of the roof of the true tympanic cavity, to which the bulla supplies a large antero-medial accessory chamber, the two communicating by a large opening. The pterygoid by a posterior splint comes to articulate with the inner side of the bulla.

In Phascolarctus one finds a tympanic bulla equally as extensive as the last, and again the external aperture of the foramen ovale is removed from the petrosal. The "foramen" is here a canal, whose inner aperture, close to the petrosal, is above the bulla, and whose outer aperture is anterior

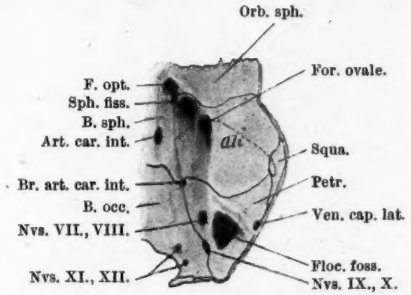

FIG. 8.—*Perameles obesula.* Right half of the cranial cavity.

to the bulla. The bulla is laterally flattened, and anteriorly appears as though formed in an enlarged posterior end of the pterygoid wing. The pterygoid bone is applied to the inner side of the bulla.

In the Wombat (Phascolomys) a very imperfect bulla tympani is formed by the squamosal, and the tympanic wing of the alisphenoid is represented by a spur which lies behind the foramen ovale.

The condition in Phascolomys approximates closely to what is found in all other mammals except some Insectivores which resemble more closely other Marsupials.

In Echidna (figs. 9 and 10) the Echidna-pterygoid has the following relations. Anteriorly it articulates with the ala temporalis (which in all probability is really processus alaris only); medial to the articulation with this last, the bone is in contact with the pterygoid, and with the palatine below this along its own inner and forward limit. Lateral to the ala temporalis it forms the median and posterior boundary of the foramen

ovale, and behind that an appreciable extent of the cranial floor, being limited here by the sphenoidal processus anterior prootici laterally, the

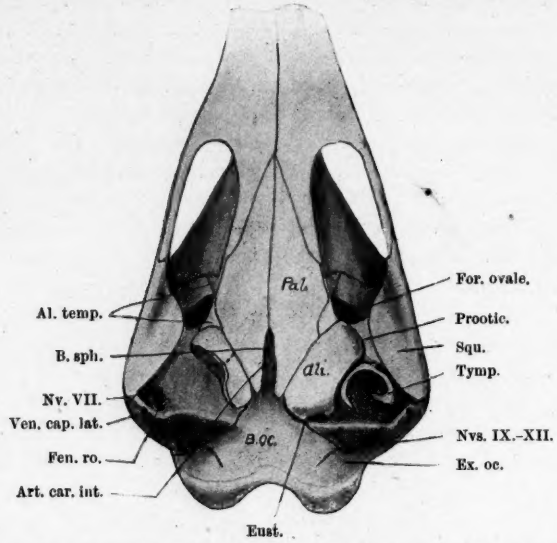

FIG. 9.—The alisphenoid has been partly removed on the right (left of figure) to show the articulation with the petrosal in the roof of the tympanum, and articulation with the same bone on the cranial aspect is indicated by a dotted line.

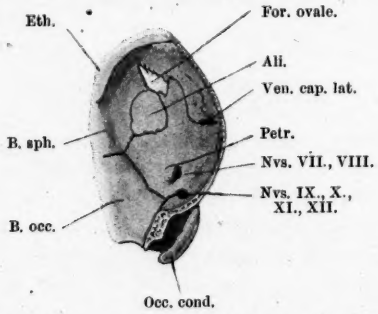

FIG. 10.—Inner aspect of right half cranial cavity of Echidna.

prootic posteriorly, and the basisphenoid medially. It is now continued back beneath the petrosal to articulate with the basioccipital. Its outer edge is free, and articulates with the tympanic. Medial to the tympanic the bone is excavated to form the inner portion of the floor, the inner wall,

medial portion of the front wall, and a small antero-medial portion of the roof of the tympanic cavity. The rest of the roof is formed by the petrosal, there being no squamosal component of the tegmen. There is no articulation between the Echidna-pterygoid and the squamosal owing to the sphenoidal flange of the prootic.

The Eustachian tube in the Marsupials issues from the tympanum, with the alisphenoid wing in front to the outer side and below, the petrosal behind to the inner side and above, and the basioccipital or basioccipito-basisphenoid suture to the inner side of the petrosal at the point of departure of the tube.

The Eustachian tube in Echidna comes through a notch, with the Echidna-pterygoid in front and below, the petrosal behind and above, and the basi-occipital to the inner side at the point where the tube leaves the two bones.

There is no doubt that the palatine in Echidna has acquired its marked extension backward to well behind the basioccipito-basisphenoid suture as an individual and purely secondary variation, so that the Echidna-pterygoid-palatine articulation is quite unimportant in the present connection.

That being so, one cannot but be convinced that the similarity of situation and relations between the marsupial tympanic wing and prototherian Echidna-pterygoid is either a most remarkable series of coincidences, or else arises phylogenetically, and the two structures are homologous.

The latter is the more reasonable view to take, and no cogent arguments can be advanced against it.

The Echidna-pterygoid, then, is an alisphenoid tympanic wing.

If, as Watson has contended, such a wing is a primitive feature in the Therian skull—and its presence in Marsupials and Insectivores certainly lends support to such a contention—it was well to impress that fact on our morphology by discarding the meaningless and misleading term "Echidna-pterygoid" in favour of alisphenoid.

To the writer it appears as probable that the prototherian alisphenoid is vestigial of an alisphenoid developed in their common ancestor to the extent to which the Marsupials retain it.

Why in the Prototheria the sphenoidal portion became aborted no explanation is offered.

I wish to acknowledge my indebtedness to Professor W. A. Haswell and Professor J. T. Wilson, who by lending me from their private libraries have placed the literature within my reach. To Professor S. J. Johnston my thanks are due, not only for the loan of books, but also for the loan of material.

Gin Gin, Queensland,
18*th June* 1917.

KEY TO LETTERING OF THE FIGURES.

Ali.	Alisphenoid.
Art. car. int.	Internal carotid artery.
B. sph.	Basisphenoid.
Eth.	Ethmoid.
Ex. occ.	Exoccipital.
F. opt.	Foramen opticum.
For. proot.	Foramen prooticum.
Front.	Frontal bone.
Mx.	Maxilla.
Orb. sphen.	Orbito-sphenoid.
Pal.	Palatine.
Petr.	Petrosal.
Pre. sph.	Presphenoid.
Sph. fiss.	Sphenoidal fissure.
Sph. memb.	Sphenoidal membrane.
Ty. and *Tymp.*	Tympanic.
V. dip.	Diploic vein.
Al. temp.	Ala temporalis.
B. oc.	Basioccipital.
Eust.	Groove for cartilaginous Eustachian tube.
Fen. ro.	Fenestra rotunda.
Floc. fossa	Floccular fossa.
F. ov. and *For. ovale*	Foramen ovale.
For. rot.	Foramen rotundum.
Ju.	Jugal.
Occ. cond.	Occipital condyle.
Ot. cap.	Otic capsule.
Par. occ. proc.	Paroccipital process.
Pl. bas.	Planum basale.
Ptery. and *Pter.*	Pterygoid.
Sph. ot. fiss.	Sphenoptic fissure.[1]
Squ. and *Squa.*	Squamosal.
Ven. cap. lat.	Vena capitis lateralis.

[1] This term is used to designate the composite sphenoidal fissure and optic foramen present in quite a few Marsupials and many Reptiles.

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THE HEART OF THE LEATHERY TURTLE, DERMOCHELYS (SPHARGIS) CORIACEA. WITH A NOTE ON THE SEPTUM VENTRICULORUM IN THE REPTILIA.

By CHAS. H. O'DONOGHUE, D.Sc., F.Z.S., *Senior Assistant in the Zoology Department, University College, London.*

THE Luth or Leathery Turtle is the largest of living Chelonians, and is of considerable interest in comparative anatomy, inasmuch as it is the sole representative of the order Atheca, an undoubtedly primitive group with a number of peculiar characters, the most remarkable being probably the shell, which is quite unlike that of any other form. Its interest is enhanced by its rarity, and, owing to its enormous size when adult, not much is known of the anatomy of its soft parts, the skeleton and muscular system alone being thoroughly known. This being the case, it is desirable that any additions that can be made to our comparatively slight knowledge of this isolated species should be recorded. Furthermore, since the observations here made differ in certain important particulars from the only others on the heart known to me, namely, those of Burne (2), it would appear useful to give another and more detailed account of this important organ. No figures of the heart have been given previously, and the accompanying ones were kindly drawn for me by Miss G. M. Woodward. I have to tender my best thanks to Dr S. F. Harmer, Keeper of Zoology in the British Museum of Natural History, for his courtesy in granting me facilities for examining the heart of a specimen recently acquired for the national collection.

The animal in question was a large female measuring 7 feet 1 inch from snout to tip of tail, and weighed $9\frac{3}{4}$ cwt. It was caught somewhere off the Scilly Islands on June 7, 1916.

References to certain points in the anatomy of Dermochelys are not frequent in zoological literature, and the first appear to be some on the alimentary canal and related viscera by Temminck (14) in 1836. These were added to considerably by Rathke (13) ten years later, who gave a description of the trachea, œsophagus, and stomach. The same author later (12) describes some of the muscles and also certain veins in a very young specimen, and this is, so far as I know, the first account of any part of the circulatory system, but does not bear on the present observations. The

muscles, more particularly those of the fore limb and girdle, were dealt with by Fürbringer (3), and again Vaillant (15) contributed a more complete account of the alimentary canal and method of feeding.

The last worker was Burne (2), who has described with accuracy and some detail a number of supplementary points in the general visceral anatomy. The muscles in particular are fully dealt with, so that the muscular system is now quite well known and a number of useful additions made to the previous accounts of the alimentary canal. What concerns us more especially is that he has described certain veins and for the first time given a description of the heart.

Before passing on to the detailed description of that organ it will be as well to indicate the points in which the present observations differ from those made by Burne.

1. This author describes the heart as being "somewhat long and narrow," whereas the present specimen was decidedly short and broad, and indeed in general proportions is similar to that of other Chelonians, *e.g.* that of *Chelydra serpentina*, as figured by Fritsch (4).

2. The apex of the ventricle is stated to taper to form a long, stout gubernaculum cordis, while I found the apex of the ventricle very bluntly rounded and the gubernaculum short, as is clearly shown in the accompanying text-figure. This may be due to the difference in age of the two specimens, since that employed by Burne was considerably younger than mine. It was undoubtedly a quite immature specimen, for its total length was only 135 cm. as against 7 feet 1 inch, and also the oviducts were imperforate; a similar condition of the heart apparently occurs in the young crocodile (*C. acutus*). Then, too, the diameter of the aortic arch on each side when flattened is given as 2 cms. instead of 3·5–4 cm. A similar difference is recorded in Chelone by Rathke (12), who found that in the embryo the heart is long as it is in most other Reptilia, while in the adult it is very broad as in the Chelonia in general.

3. The walls of the auricles are said to be "very thin in comparison with *Chelone midas*, and show very little trabecular structure." In the present specimen the trabecular structure is quite strongly marked and the walls appear actually thicker, *i.e.*, taking into account the difference in size, relatively quite as thick as in *C. midas*.

4. In both specimens the actual cavity in the ventricle is astonishingly small, but the ventricular wall forming the whole of the lower half or two-thirds of the ventricle was found to be extremely spongy, and blood coagula were present in its lacunæ all through it right down to the apex. Burne, on the other hand, found this part of the heart to consist "practically of solid muscle."

These two points (3 and 4) again may perhaps be due to the one animal being so much younger than the other.

5. The left auricle is noticeably smaller than the right, but the difference is not so great as to describe it as being "relatively very small—not more than a quarter the size of the right." The state of distension of the auricles at the time of death probably influences their apparent size to a very appreciable extent.

6. A further point to be noted, for which it is more difficult to find an explanation, is the statement that "the carotids, 7 cm. above their origin from the innominate artery, suddenly dilate to at least twice their original diameter and then very gradually narrow again towards the head." Unfortunately, when the heart was removed, before I had an opportunity of examining it, the great arterial and venous trunks were all cut off fairly close to the heart, so that I have not been able to confirm the presence of this decidedly unusual condition. In the portions of the carotids present, 8·5 cm. in length, there is no indication whatever of any dilatation.

In other particulars I am able to confirm Burne's description.

The heart of the present specimen of Dermochelys (*vide* text-fig. 1) is a very large massive organ whose general form is undoubtedly Chelonian and corresponds most nearly to that of *Chelydra serpentina*, with which it agrees fairly closely, as a comparison between the figures given here and those of Fritsch (4) will show.

A very well-developed sinus venosus is present situated to the right of the middle line, and opening, as always in the Reptilia, into the right auricle. The sinus was actually cut into in removing the heart, with the result that it is not quite complete. The two pre-caval veins, the right and the left, are intact, but the post-caval is missing, together with a portion of the dorsal wall of the sinus. The pre-caval veins are very large, the left being 6 cm. in diameter when flattened, and the right about 1 cm. larger. The conformation of the remaining parts of the sinus, however, are such that they indicate quite clearly the position of the post-caval vein, which has therefore been restored in the drawing for the sake of completeness. It opened quite close to the left pre-caval vein at the left postero-lateral corner of the sinus. In *Chelydra serpentina*, Fritsch (*l.c.*) figures two hepatic veins opening into the base of the post-caval, and in addition two quite large independent hepatic veins opening directly into the sinus venosus at its right antero-lateral border only a short distance from the base of the right pre-caval vein. This part of the sinus is absent in my specimen, so that it is not possible to say definitely whether they are present in Dermochelys or not. If they are present, however, it is evident that they were relatively very much smaller than in Chelydra, and for this reason they have been

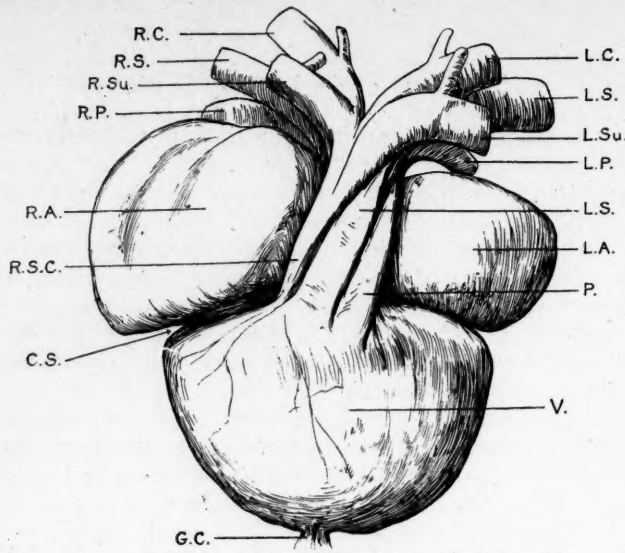

FIG. 1A.—Ventral view of the heart and main vessels of Dermochelys.
Ad nat. Drawn by Miss G. M. Woodward.

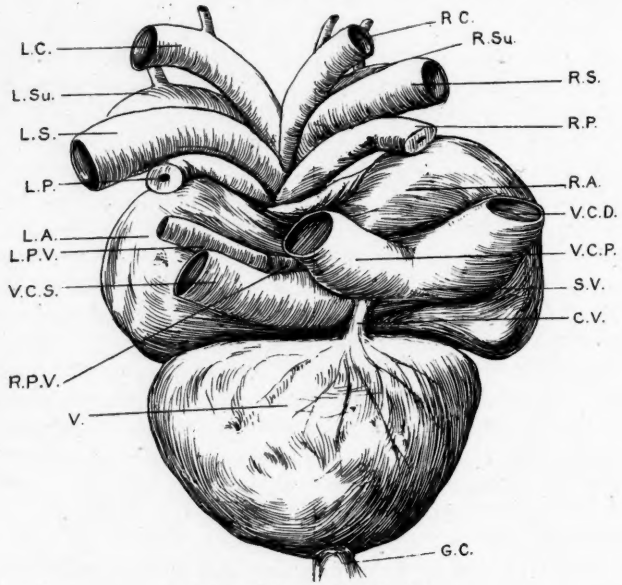

FIG. 1B.—Dorsal view of same.
Ad nat. Drawn by Miss G. M. Woodward.

C.S., coronary sulcus; C.V., coronary vein; G.C., gubernaculum cordis; L.A., left auricle; L.C., left carotid artery; L.P., left pulmonary artery; L.P.V., left pulmonary vein; L.S., left systemic arch; L.Su., left subclavian artery; P., pulmonary arch; P.V., pulmonary vein; R.A., right auricle; R.C., right carotid artery; R.P., right pulmonary artery; R.P.V., right pulmonary vein; R.S., right systemic artery; R.S.C., right systemico-carotid trunk; R.Su., right subclavian artery; S.V., sinus venosus; V., ventricle; V.C.D., right pre-caval vein; V.C.P., post-caval vein; V.C.S., left pre-caval vein.

omitted from the drawing. Into the sinus venosus, to the right of the left pre-caval vein and posterior to the post-caval, opens the coronary vein, which appears as a very tough vessel about 1·5 cm. in diameter, passing across the coronary sulcus.

The sinus venosus opens into the right auricle by a sinu-auricular aperture about 12 cm. in length starting at the right posterior corner of the auricle and running forwards and outwards at an angle of about 45° to the long axis of the heart. It is guarded by two valves along its sides which are continued on along the auricular wall for a short distance beyond the opening as flaps.

As pointed out above, there is a decided but not great difference in size between the auricles. They are separated by a well-developed septum auriculorum, which is complete in Dermochelys and not perforated as it is stated to be by Huxley (8, p. 264) in some Chelonia. The left auricle is a large sac whose actual size varies with its distension, but in the specimen measures about $14 \times 10{\cdot}5$ cm. It is thin-walled as compared with the ventricle, but considerably stouter than the sinus venosus, and in its postero-dorsal corner reaches a thickness of about 1·5 cm. Inside, particularly on its dorsal aspect, it has a number of well-marked muscle strands, the musculi pectinati. The two pulmonary veins open into the middle of its median dorsal border by a single small aperture not guarded by any well-marked valves. The right auricle, as already noted, is considerably larger, measuring in the specimen $17{\cdot}5 \times 15$ cm., and is also thicker walled. Its walls in the latero-dorsal region attain a thickness of about 2·5 cm., and are plentifully supplied with muscle strands. The position of the sinu-auricular aperture with its large valves has been described.

The ventricle is an extremely stout sac of a blunt, rounded triangular shape, measuring along its base by the coronary sulcus about 24 cm. and from this border to the apex about 17 cm. The walls are enormously thick and muscular, reaching a thickness in the apical region of as much as 10–11 cm. They are entirely composed of a number of muscular trabeculæ which are woven together to form a loose, spongy tissue in whose spaces are blood-clots. No traces of definite columnæ carneæ or musculi papillares were found, and if present at all must have been small and removed in clearing the large solid clot with which it was filled. To the apex were attached numerous tough, stout muscular bands, some separate and others united by a binding tissue constituting a very well-developed gubernaculum cordis such as has been described by Beddard (1) in Tupinambis, and stated by him to be general in Lacertilia, and also noted by other writers in other species of reptiles. This as it were ties the ventricle to the pericardium, by a reflexion of which it is covered.

The two auricles open independently into the ventricles by quite large slits at their postero-mesial corners; and although the apertures are fairly close together, they are absolutely separated from one another by enormously strong moderately complex valves. Guarding the left auriculo-ventricular aperture is a strong oval valve about 1 cm. thick, of almost cartilaginous consistency. It does probably contain cartilage, but I did not wish to damage the specimen more than necessary. The valve is attached to the latero-ventral wall, its free edge hanging down into the ventricle. This causes the aerated pulmonary blood entering the ventricle to be sent across to its left side. Parallel with this is a similar but stronger and much larger valve guarding the right auriculo-ventricular orifice. Its position agrees closely with the partly muscular, partly cartilaginous septum in the turtle *Chelone midas* as described by Huxley (8), and so we can recognise a space on either side of it which that author has termed the cavum arteriosum on the left and the cavum venosum on the right. This description is quite accurate, as can be seen at once by the dissection of a heart of Chelone. This valve in Dermochelys is unlike that on the left or that in the turtle in that it is curled upon itself to form a deep trough whose concavity is directed anteriorly. The non-aerated venous blood enters in front and to the left of this valve, and is consequently forced out to the left side of the ventricle.

Again as in the turtle, a strong thick band of the ventricular muscle, constituting a distinct though incomplete ventricular septum, is also present, and, running more transversely than the valves, is so arranged that when the ventricle is contracted it practically cuts off a portion of the cavum venosum, and this chamber has been termed by Huxley (*l.c.*) the cavum pulmonale. The cavity of the ventricle is thus divisible into three portions: a right ventro-lateral cavum venosum, a left dorso-lateral cavum arteriosum, and an almost entirely separate division of the former, the cavum pulmonale.

The anterior end of the incomplete septum is also tough like cartilage, and under it, *i.e.* ventral to it, is situated the opening of the pulmonary trunk, so that the venous blood is poured into the heart quite close to the aperture of this vessel. Clear of the septum, *i.e.* lateral to it, lies the opening of the left systemic arch. This is to the side where the septum is not complete, and therefore when the ventricle is distended it is near the region where the two bloods mingle, and so may receive aerated as well as non-aerated blood. When the ventricle is contracted, however, it opens from the small right ventro-lateral chamber, as does the pulmonary arch.

The large common trunk giving rise to both the right systemic and

the carotid arches, on the other hand, opens from the ventricle completely on the dorsal side of the septum, and so from the remaining part of the cavum pulmonale, but still in that cavity and on the right side of the right auriculo-ventricular valve. Thus it follows that no arterial trunk comes off from the cavum arteriosum, and the aerated blood must pass through the corner of the cavum pulmonale on its way out. The right systemic and carotid trunk is, then, more or less completely separated from the opening of the other arterial trunks during ventricular systole. During diastole, in spite of its opening lying in the cavum venosum, the

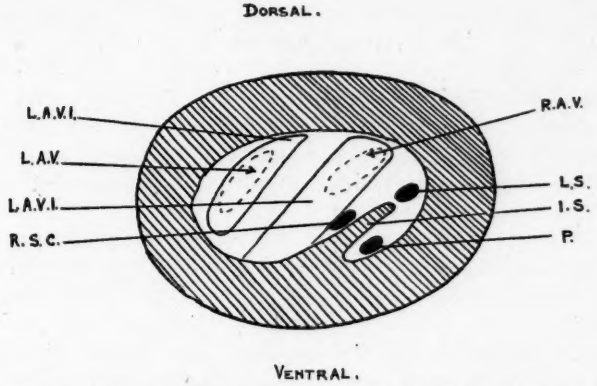

FIG. 2.—Diagram of the valves, septum, and ventricular apertures of Dermochelys, viewed from the posterior aspect.

I.S., incomplete septum; L.A.V., left auriculo-ventricular aperture under L.A.V.I., valve of same; L.S., opening of left systemic trunk; P., opening of pulmonary trunk; R.A.V., right auriculo-ventricular aperture under R.A.V.I., valve of same; R.S.C., opening of right systemico-carotid trunk.

trough-like right auriculo-ventricular valve directs the non-aerated blood away from the systemico-carotid trunk, while there is nothing to prevent it receiving blood from the left auriculo-ventricular opening.

There is little doubt, then, that the non-aerated blood from the cavum venosum leaves mainly by the pulmonary arch, and the aerated blood practically entirely by the right systemico-carotid trunk. The left systemic appears to convey in the main non-aerated blood, but there is no reason to suppose that it does not also have a slight admixture of aerated blood. It is therefore obvious that functionally there is a fairly complete separation of the two blood-streams in the ventricle.

In his excellent description of the turtle heart, which I have followed to a certain extent above, Huxley makes the main division of the ventricle,

that by the auriculo-ventricular valve, into cavum arteriosum and cavum venosum. It would, I think, be better, for reasons that will appear obvious in what follows, and also on account of its functional importance, to throw the stress more on the division brought about by the ventricular septum. Thus we have a cavum pulmonale, from which only the non-aerated blood leaves the heart, and a cavum systemico-caroticum, from which practically only aerated blood leaves. The other division into cava arteriosum et venosum is to be looked on as a functional complication of the auriculo-ventricular valve necessitated by the incompleteness of the true ventricular septum, and not of importance in the future complete subdivision of the ventricle.

The bases of the arterial trunks are guarded in a typical manner by semilunar valves.

The two subclavian arteries arise from the corresponding carotids quite near their base.

The heart of Dermochelys, then, is typically Chelonian, and agrees fairly well externally with that of *Chelydra serpentina*, and internally is much like *Chelone midas*.

The Septum Ventriculorum.

During the foregoing investigation of the heart of Dermochelys, the hearts of a number of other Reptilia, in my own possession, at University College, the Natural History Museum, and the Royal College of Surgeons, were examined for purposes of comparison. Furthermore, the heart of the Tuatara (*Sphenodon punctatus*), of which animal I hope shortly to publish a full account of the circulatory system, was also examined in a series of specimens kindly placed at my disposal by Professor A. Dendy, F.R.S., to whom I wish to tender my thanks. As a result of these inquiries, several interesting facts came to light, and it soon became evident that the statement of Goodrich (6), who lays some stress on the position of the septum ventriculorum in his scheme of classification of the Reptilia, was incomplete, and indeed, in respect of certain members of that class, somewhat misleading. This author states (p. 271) that ". . . in the Reptilia the interventricular septum tends to divide the chamber into a left cavity leading to the base of the systemic arch, and a right cavity leading to the base not only of the pulmonary but also of the left systemic arch"; and further indicates the same idea graphically in a very clear diagram on p. 273, which he states applies to Reptilia in general, excluding the Crocodilia. In order to clear up this point, if possible, the relation of the openings of the aortic arches to the septum ventriculorum was examined in the following animals:—

RHYNCHOCEPHALIA: *Sphenodon punctatus.*

LACERTILIA: *Varanus salvator, Heloderma horridum, Lacerta viridis, L. agilis, Phrynosoma cornuta, Scincus tridactylus, Chameleo* sp.? *Tiliqua scincoides.*

OPHIDIA: *Python tigris, Boa constrictor, B. murina, Crotalus horridus, Tropidonotus natrix.*

CHELONIA: *Chelone midas, Testudo græca, Dermochelys coriacea.*

CROCODILIA: *Crocodilus americanus, Crocodilus* sp.? (a smaller specimen), *Caiman* sp.?

It soon became evident that each group possessed its own peculiar and more or less characteristic arrangement of the arches and septum. They will therefore be treated briefly in groups from the most to the least specialised.

CROCODILIA.—In the first place, it is only in the Crocodilia that a complete septum ventriculorum is present. Here, taking *Crocodilus americanus* as a typical representative, we find the septum is quite complete, and it runs from the right latero-dorsal to the left latero-ventral wall of the ventricle, although it is almost in the dorso-ventral plane. The two ventricular cavities are thus a right lateral, slightly ventral in position, and a left lateral, slightly dorsal. The common trunk of the right systemic and carotid arches, which for convenience may be termed the right systemico-carotid, comes off the left chamber, into which the left auricle pours the aerated blood; while the left systemic and the pulmonary arches come off from the right chamber, and so convey nothing but non-aerated blood derived from the right auricle.

This condition, as pointed out by Goodrich, will lead directly to that in birds by the loss of the left systemic arch.

Similar relations were found in *Crocodilus* sp.? and *Caiman* sp.?, and also in *Alligator lucius*, as described by Gegenbaur (5, p. 387).

CHELONIA.—The condition in Dermochelys has been fully described above, and it will be seen that, although the septum is incomplete, yet it bears the same relation to the pulmonary and right systemico-carotid arches as in Crocodilia. The difference, due to the incompleteness of the septum, is that, as the opening of the left systemic arch lies right opposite to the free end of the septum, there is always the possibility that a certain amount of aerated blood may enter it during diastole. In the crocodile, of course, this is quite impossible.

The ventricle of Testudo and of the turtle, as clearly stated by Huxley (*l.c.*), is similarly divided, and the relations of the septa and vessels are indicated diagrammatically in the accompanying figure.

OPHIDIA.—*Python tigris* may be taken as a representative of this group.

The interventricular septum is very well developed and attached to the left dorso-lateral side of the ventricle, running from base to apex and directed towards the right ventro-lateral wall. Thus it runs in a direction entirely different from that of the septum in either Crocodilia or Chelonia—in fact, nearly at right angles to it,—and divides the ventricular cavity, at any rate in systole, into a right dorso-lateral and a left ventro-lateral

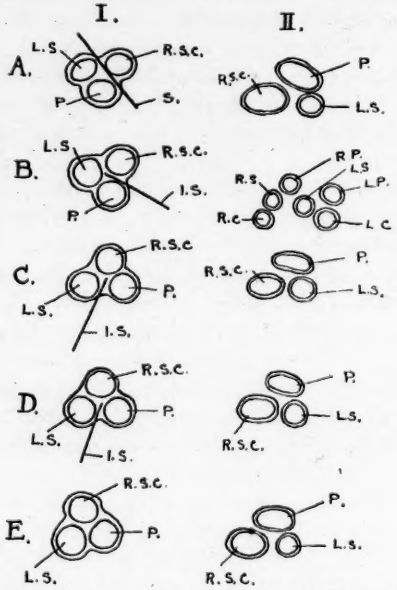

FIG. 3.—Diagrammatic representation of the arterial trunks (I.) close to the ventricle, (II.) near the top of the auricles, in (A) *Crocodilus americanus*, (B) *Chelone midas*, (C) *Python tigris*, (D) *Varanus salvator*, and (E) Sphenodon.

I.S., Incomplete septum; L.C., left carotid artery; L.P., left pulmonary artery; L.S., left systemic arch; P., pulmonary arch; R.C., right carotid artery; R.P., right pulmonary artery; R.S., right systemic artery; R.S.C., right systemico-carotid trunk; S, complete septum.

chamber. It is tough and fibrous at the anterior end, but becomes somewhat spongy like the ventricular wall near the apex, and it is possible that the two chambers may be in communication one with another even during systole through these pores. Another great difference between this and the foregoing two groups is the position of the arterial apertures. From the right dorso-lateral chamber come off not only the right systemico-carotid but also the left systemic arch. Only the pulmonary arch, on the

other hand, comes off from the left ventro-lateral chamber. The openings of the right and left systemic arches lie close together, only separated by the union of their walls to form a common band; whereas the pulmonary aperture is quite distinct, and situated on the other side of the incomplete septum.

Both auricles open into the right latero-dorsal chamber, the left auricle opening fairly dorsally about the middle of its anterior end, and so it lies a short distance from the openings of both the right systemico-carotid and the left systemic arches. Thus the aerated blood can pass straight from auricle to these trunks. The right auriculo-ventricular aperture lies in the most ventral corner of the right lateral chamber, quite close to the openings of the right systemico-carotid and left systemic, and also to the top of the incomplete septum. It is, however, guarded by a large bi-lobed valve running somewhat transversely. The anterior flap of the valve, when open during auricular systole, partly or perhaps completely closes the systemic arches; while the posterior valve is of a somewhat curious spout shape that directs the non-aerated blood across the septum to the left lateral chamber.

Although the exact *modus operandi* of the right auriculo-ventricular valve cannot be determined in dead hearts, there seems little doubt that during auricular systole the major part of the non-aerated blood is sent into the left lateral chamber, from which the pulmonary arch arises. The right lateral chamber, on the other hand, is filled mainly with aerated blood, and may perhaps receive any overflow of non-aerated blood from the smaller left chamber.

Similar conditions also obtain in the other snakes examined, and the external twisting of the arterial trunks in *Tropidonotus natrix* has already been pointed out (9).

Lacertilia.—A large heart of *Varanus salvator* in the collection of the Royal College of Surgeons was examined, and can be regarded as more or less typical of the group. The septum here, as in the Ophidia, runs from the left latero-dorsal wall of the ventricle across towards the right latero-ventral wall, but is decidedly more dorso-ventral in position than in the Ophidia. As in that group, however, it is incomplete, so that it is only during systole that the ventricular would appear to be completely divided into a right lateral, slightly dorsally situated chamber and a smaller left lateral chamber lying slightly ventrally. The left chamber again gives off only the pulmonary artery, while the right systemico-carotid and left systemic arches both come off from the larger right chamber. Into this chamber also, as in Ophidia, both the auricles open. Their valves are much as in *Python*—*i.e.* the left opens centro-dorsally, while the right opens in the ventral corner, and by means of its valves discharges its non-

aerated blood past the openings of the right systemico-carotid and left systemic arteries across the septum into the left chamber, and so to the pulmonary arch.

Parker (11, p. 174) states that in the lizard, *Lacerta viridis*, the two aortic openings lie on the right, and are separated from the pulmonary opening on the left by a muscular partition. This has been verified, and is also true of *L. agilis*. A similar condition is shown by Wiedersheim (16), in a figure on p. 407, in *L. muralis*. In these Lacertidæ, however, the partition is in a less developed condition than in Varanus. For the information regarding *Tiliqua scincoides* I am indebted to Professor J. P. Hill, F.R.S.: it is typically Lacertilian. The other species also conform to this general plan, but there appears to be a greater variation in the degree of development of septum ventriculorum among the Lacertilia than in other Reptilia—not an unexpected thing in view of the fact that they are undoubtedly a less specialised group than any other of the reptiles, with the exception, of course, of the Rhynchocephalia.

Thus the conditions in Ophidia and Lacertilia are quite different from what is implied by Goodrich both in the extract given above and in the diagram. The ventricle in these two groups, containing by far the greater number of living species of reptiles, is indeed partially divided into a right and left chamber, but the two systemic arches come off from the right side and the pulmonary arch alone comes off from the left. There is thus a considerable difference in the relation of the septum to the arterial trunks between the Ophidia and Lacertilia on the one hand and the Crocodilia and Chelonia on the other. Not only is there a greater twist on the arterial trunks, which leave the top of the heart in relatively the same position, while the pulmonary leaves the ventricle more to the right in the latter, but the septum is actually situated on opposite sides of the pulmonary artery. In Ophidia and Lacertilia it lies between the pulmonary and left systemic, while in Crocodilia and Chelonia it lies between the pulmonary and right systemico-carotid.

Another striking and important difference which has not been emphasised formerly is that, whereas in the Crocodilia and Chelonia, as in birds and mammals, the aerated blood is poured into the left side of the ventricle, in Ophidia and Lacertilia the reverse is the case and the aerated blood passes into the right ventricular chamber.

Rhynchocephalia.—In view of the fact that the aortic arches in Sphenodon are, as has been shown recently (10), in a more primitive condition than in other reptiles, it was hoped that an examination of the ventricle might throw some light on the question of the septum. Four hearts were dissected, and two were examined in serial sections. The first

series had been cut at 10μ by Professor Dendy, and the second was cut for this purpose at 20μ. They have indeed shown a simple condition. There is no septum ventriculorum comparable with that in the other Reptilia; although the ventricular wall is irregular, no fold appears to correspond with this septum. Moreover, though the exact structure has not yet been satisfactorily determined, it appears as if the three arterial arches come off from a sort of extension of the ventricle in which extensions of their ends form a sort of valve. If this should prove to be the case, it may be that we are here dealing with a rudimentary conus, a structure well represented in the amphibian heart, but which Greil (7) has shown is absorbed into the ventricle in the Reptilia. The state of preservation of the interior of none of the hearts has allowed me to speak definitely on this point.

The pulmonary arch lies on the left of the other two openings which appear to come off from a short common stem situated to the right. Thus we meet with a condition more simple than in other Reptilia, but which, nevertheless, is distinctly reptilian. It also resembles the Lacertilia and Ophidia more closely than the other two groups, since, although the means are not clear, it is obvious that the non-aerated blood leaves the right side of the heart and the aerated blood the left side.

Greil (*l.c.*, p. 227), in an instructive paper on the development of the heart in the Vertebrata, concludes: "Wie bereits in der Einleitung bemerkt wurde, zeigen die Herzen der untersuchten Reptilien nur unterschiede graduelle Natur. Diese unterschiede betreffen vor Allen den Bau und die Ausbildung der Scheidewände im Inneren der Kammer, und es lassen sich die Herzen der Reptilien in dieser Hinsicht gewissermassen zu einer Entwicklungsreihe zusammenstellen, an deren Aufang das Herz von Hatteria und der niederen Saurier, und deren Ende das Herz der Crocodilier zu stehen kommt." This passage is correct to a certain extent, but it certainly does not indicate sufficiently clearly the primitiveness of the heart in Sphenodon, in which the septum does not appear to have started; nor does it notice the fact that the position of the septum when present varies considerably in different groups.

In the Reptilia, then, we have two distinct types of heart. The one, found in Chelonia and Crocodilia, in which the aerated blood is found on the left side of the septum whether it is complete or not, can easily be regarded as leading to the condition in birds. The other is characteristic of Ophidia and Lacertilia, and has the non-aerated blood on the left side of the septum, and thus, as Goodrich points out—although his statement of the relation of septum to the arches is open to objection,—cannot in any way lead to the condition in a mammal, where of course the non-aerated blood is in the right ventricle.

The Rhynchocephalia, in as far as the position of the aerated blood leaving the heart, are as it were definitely committed to a Lacertilian as opposed to a Chelonian or Crocodilian line of development, yet retain certain primitive features. The absence of a septum is one point, and the fact that the two systemic arches appear to come off from a short common trunk; for, as Goodrich remarks (p. 271), "the Theropsidan and Sauropsidan types must have evolved from more symmetrical primitive type, in which the ventricle and aortic arches were both single." Here, then, in Sphenodon, although still removed from this ideal condition, we find undoubted hints as to its existence and a certain amount of approximation to it.

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